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Bulletin of the
British Museum (Natural History)

The tick collection (Acarina: Ixodoidea) of the Hon. Nathaniel Charles Rothschild deposited in the Nuttall and general collections of the British Museum (Natural History)

James E. Keirans

With a Foreword by the Hon. Miriam Rothschild

Zoology series Vol 42 No 1 25 March 1982

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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The tick collection (Acarina: Ixodoidea) of the Hon. Nathaniel Charles Rothschild deposited in the Nuttall and general collections of the British Museum (Natural History)

James E. Keirans

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With a Foreword by the Hon. Miriam Rothschild

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Synopsis

The Hon. N. C. Rothschild achieved worldwide fame for his study of the Siphonaptera. During the early part of this century he also made a significant collection of ticks which he gave to Professor George H. F. Nuttall at Cambridge University. Upon Nuttall's death, the collection was given to the British Museum (Natural History) and is kept as a separate entity.

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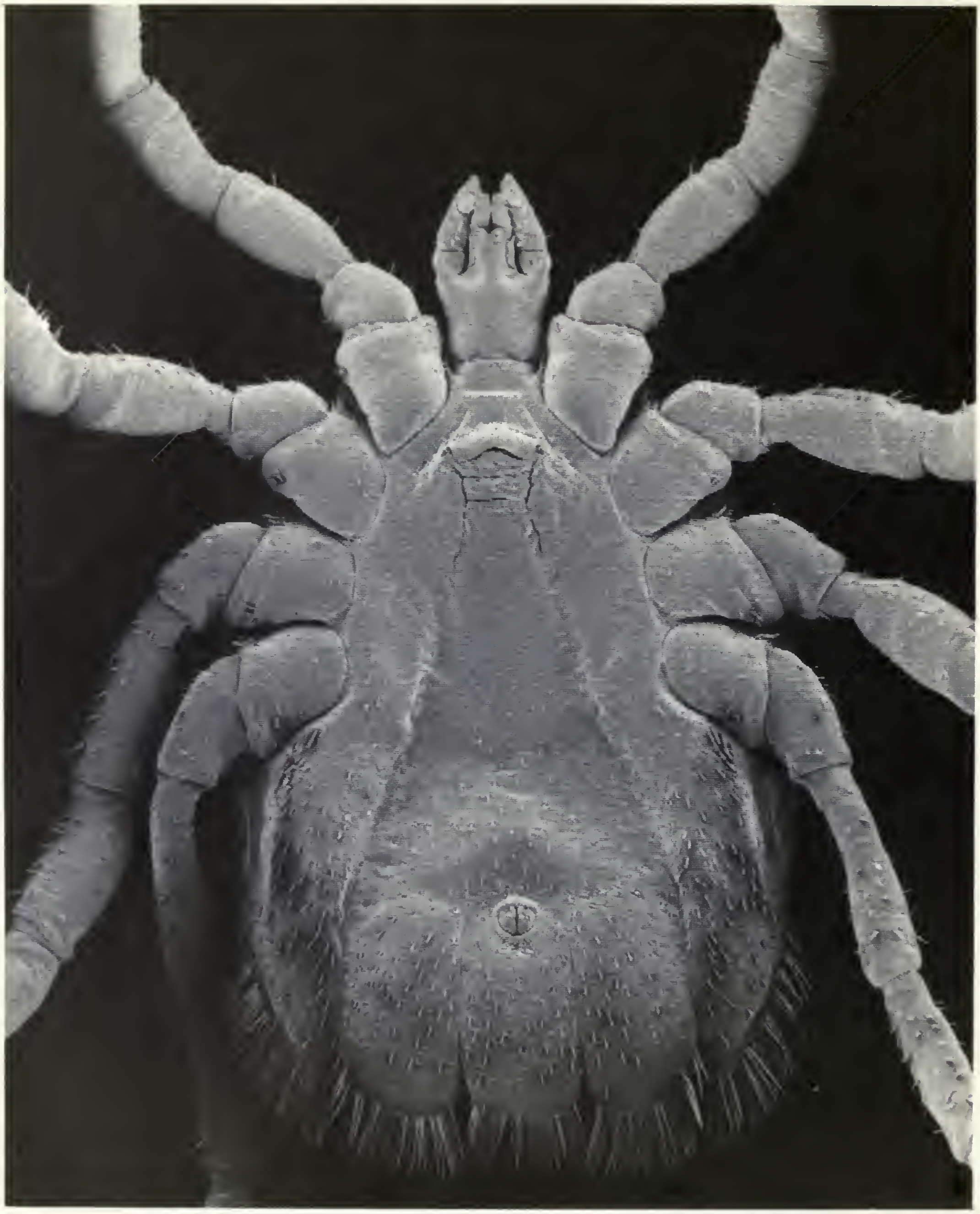

Male *Ixodes uriae* White, 1852. (Ixodoidea: Ixodidae). A tick with a circumpolar distribution in both the northern and southern hemispheres. It is ectoparasitic on a variety of seabirds and to date, twenty different arboviruses have been recovered from this species.

In addition, Rothschild on numerous occasions between 1911 and 1923 deposited ticks in the British Museum (Natural History). Herewith are recorded the 197 tick collections of the Hon. N. C. Rothschild plus one of the Hon. Walter Rothschild deposited in the Nuttall collection and the 156 collections in the general collection of the British Museum (Natural History).

Foreword

In 1913 N. C. Rothschild presented his collection of 'Siphonaptera and other parasitic insects' to the British Museum (Natural History). One of the conditions attached to the gift read as follows: 'The Trustees shall so soon as the said collection comes into their hands or is placed under their control and as soon as the funds placed at their disposal by Parliament will allow cause to be made and published a catalogue giving the names and full number of specimens of each species of parasitic insect contained in the said collection.'

Over 60 years has now elapsed since the collection was accepted, but the catalogue has not yet been completed. Although ticks are arthropods, they are not insects, but this group of animals, along with a number of mites, was included in the collection.

During my period of Trusteeship of the British Museum (Natural History) I had the opportunity of discussing this problem with Harry Hoogstraal, and he suggested that James Keirans might undertake to catalogue the Rothschild ticks. To my great delight he agreed to do this, although the task proved more time-consuming than we had at first anticipated. This was because the Rothschild Collection had not been preserved as a single unit, and the ticks, along with the Nycteribiidae, Cimicidae, Hippoboscidae and other smaller groups, had been distributed in the general collection and, in addition, had not all received Museum accession numbers.

Although these circumstances added enormously to James Keirans' labours, they made the compilation of this Catalogue even more necessary and valuable. Until those who are engaged in ecological and medical research come to use museum material such as this, no one can really appreciate the immense boon of well-catalogued individual collections.

Since, between 1900 and 1910, N. C. Rothschild had given Professor Nuttall the bulk of his tick material*, it was considered more appropriate to merge the two catalogues into one, and the manuscript was therefore divided into two parts: **I**, the specimens collected by Rothschild, now in the Nuttall collection; and **II**, the specimens donated by Rothschild to the British Museum (Natural History). The ticks in the general collection have been added—a course we followed when cataloguing the fleas (G. H. E. Hopkins & M. Rothschild, Vols. I–V, 1953–1971) and the Nycteribiidae (Oscar Theodor, 1967).

It will be noted that Walter Rothschild contributed one specimen to this collection. It has not usually been appreciated that N. C. Rothschild's brother also added considerably to the flea material, although he did not describe any species himself. The N. C. Rothschild donations of Nycteribiidae to the British Museum contained 56 undescribed species, and the Ixodoidea collections 10. The two brothers and their collaborators described over 5000 new species, but they probably collected twice that number of animals new to science.

James Keirans has added greatly to the value of this compilation by providing information concerning the viruses and in certain cases rickettsiae of which the Rothschild ticks are known vectors.

The illustration depicts a male specimen of *Ixodes uriae* White, one of the most spectacular species, adorned with a handsome fringe along the posterior margin, which has the dubious distinction of carrying at least 20 known viruses in five different serogroups.

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*After the sudden death of Professor Nuttall in December 1937 his collection was presented to the British Museum (Natural History) by the Molteno Institute. In accordance with the terms of the gift this collection is maintained as a discrete entity.

Altogether the meticulous care and accuracy with which James Keirans has completed this catalogue is beyond praise.

Miriam Rothschild

Introduction

Early in the twentieth century, Nathanial Charles Rothschild acquired a large tick collection, primarily from collectors who, knowing of his great interest in fleas, would send him not only that group but also other ectoparasites including flies, bugs, and ticks.

He deposited his tick collection in two institutions; the Molteno Institute for Research in Parasitology, Cambridge University, where Professor G. H. F. Nuttall made the original determinations of all tick material, and the British Museum (Natural History), where Mr A. S. Hirst made the tick determinations. As mentioned earlier, the Nuttall collection is now at the BM(NH).

Because the Nuttall collection is kept as a discrete entity, separate from but housed with the BM(NH) collection, parts of Rothschild's tick collection are in each of the above collections. This catalogue is also divided into two sections: Part I, Rothschild tick donations to the Nuttall collection; Part II, Rothschild tick donations to the BM(NH).

The systems for numbering tick collections are different for the two sections. In Part I, the number used is that given by Professor Nuttall to a collection. The first entry is N (Nuttall) 72 followed by N73, N74, etc., in ascending sequence, first for existing specimens, then for specimens which are now missing. Each Nuttall number is followed by a Rothschild collection number or the word 'None' if the collection received no Rothschild number. A Nuttall number refers to a handwritten entry in Professor Nuttall's tick catalogue, which is now kept in the Arachnida and Myriapoda Section of the BM(NH). The locality and host data are cited in their modern forms, but where these could not be established Nuttall's own entries are quoted.

One additional point should be made relating to the Nuttall collection forming Part I. Nathaniel C. Rothschild donated all specimens recorded in Part I with the single exception of N888 which was donated by his brother, the Hon. Walter Rothschild, to the Entomological Research Committee and subsequently to Professor Nuttall.

Collections in Part II are entered alphabetically by genus, first Argasidae, then Ixodidae. All information is presented as in Part I with the exception that replacing a Nuttall and Rothschild number will be a British Museum (Natural History) registration number. Where no registration number was given to a collection, the word 'None' will appear. I have given each collection a set of Keirans numbers, K1-K156. These numbers, along with the Nuttall numbers from Part I, will allow the reader to use the tick species, locality, and host lists and refer back to individual collections within Parts I and II.

Throughout the text, citations are given to publications which mention a particular taxon. My comments are presented within square brackets [ ]; those comments by Nuttall or some other investigator are cited within square brackets enclosed by quotation marks '[ ]'.

PART I

Rothschild specimens donated to the Nuttall collection

Species of Ixodoidea represented in the Nuttall collection, British Museum (Natural History), donated by the Hon. N. C. Rothschild

Nuttall numbers follow each species. Numbers in parentheses refer to missing collections. Thus, validity of original determinations is unverified.

ARGASIDAE

Argas boueti Robaud and Colas-Belcour 1164
Argas persicus (Oken) 589, 590, (3536))
Argas reflexus (Fabricius) (3159)
Argas vespertilionis (Latreille) 591, 592, 593, 1151, 1152, 1153, 1163
Argas sp. 1154, (1388)

Ornithodoros capensis Neumann group 594
Ornithodoros moubata (Murray) 595

Otobius megnini (Dugès) (596)

IXODIDAE

Amblyomma albolimbatum Neumann (78), 567, 569
Amblyomma australiense Neumann 547
Amblyomma cajennense (Fabricius) 557, 648
Amblyomma clypeolatum Neumann (75)
Amblyomma compressum Macalister 564
Amblyomma cyprium Neumann 73, 565
Amblyomma decoratum C. L. Koch (93)
Amblyomma dissimile C. L. Koch 568
Amblyomma gemma Dönitz 558b
Amblyomma geoemydae (Cantor) 545
Amblyomma hirtum Neumann (397)
Amblyomma longirostre (C. L. Koch) 560
Amblyomma marmoreum C. L. Koch (77), 570
Amblyomma ovale C. L. Koch 562, 566
Amblyomma pecarium Dunn 557
Amblyomma tholloni Neumann 559
Amblyomma triguttatum C. L. Koch 546, (551), 552, 553
Amblyomma varium C. L. Koch (3351)
Amblyomma sp. 74, (76), (544), 633, 1166, 1386, 1391, 1392, 1393, 1394, 1396, 1397

Aponomma decorosum (L. Koch) 550
Aponomma gervaisi (Lucas) (92), (548)
Aponomma gervaisi var. *lucasi* (Warburton) (90), (91)
Aponomma hydrosauri (Denny) 556
Aponomma varanensis (Supino) 554
Aponomma sp. (571), 3138

Boophilus decoloratus (C. L. Koch) (3157)
Boophilus microplus (G. Canestrini) 588

Dermacentor albipictus (Packard) 666, 1105, 1497, 1498, 1499, 1500, 1501, 1502, 1503
Dermacentor andersoni Stiles 1387, 1390, 3502
Dermacentor reticulatus (Fabricius) 3160
Dermacentor rhinocerinus (Denny) 555, 563
Dermacentor sp. 3330

Haemaphysalis bispinosa Neumann 574, 582, 583, 892
Haemaphysalis campanulata Warburton 579
Haemaphysalis celebensis Hoogstraal, Trapido and Kohls 72
Haemaphysalis elongata Neumann 670
Haemaphysalis erinacei Pavesi 3537, 3538, 3539
Haemaphysalis humerosa Warburton and Nuttall 669
Haemaphysalis hystricis Supino 572, 573, 575, 576
Haemaphysalis indica Warburton 575x
Haemaphysalis leachi (Audouin) (539), 577, 578
Haemaphysalis punctata G. Canestrini and Fanzago 580
Haemaphysalis tiptoni Hoogstraal 670
Haemaphysalis sp. 581

Hyalomma aegyptium (Linnaeus) 549, 561
Hyalomma rufipes C. L. Koch 558a, 888 (W. Rothschild)
Hyalomma syriacum C. L. Koch (3139), (3140), (3141)
Hyalomma truncatum C. L. Koch 1167
Hyalomma sp. 1398, (3136)

Ixodes australiensis Neumann 645, 646
Ixodes boliviensis Neumann 637
Ixodes brunneus C. L. Koch (396)
Ixodes cookei Packard 1504
Ixodes fecialis Warburton and Nuttall 650, 1211, 1213
Ixodes frontalis (Panzer) 523
Ixodes hexagonus Leach (216), (217), (298), (322), (324), 597, 598, 599, 600, 601, 602, 603, 604, 606, 607, 608, 609, 610, 611, 612, 613, (674), (746), 1067, 1159, 1160
Ixodes holocyclus Neumann 643, (644), 1212
Ixodes lividus C. L. Koch 605, 1068

Ixodes loricatus Neumann 638, 639, 640, 641
Ixodes luciae Senevet 647
Ixodes nitens Neumann 360
Ixodes putus (O. Pickard-Cambridge) (516), (517), (518)
Ixodes ricinus (Linnaeus) (509), (628), (629), (630), (631), (632), (656)
Ixodes rothschildi Nuttall and Warburton 634
Ixodes rubidus Neumann 826
Ixodes scapularis Say 626
Ixodes texanus Banks 1399
Ixodes trianguliceps Birula 619, (620), 621, 622, 623, 624, 625, 1069, 1161
Ixodes unicavatus Neumann (395), 652, 667
Ixodes uriae White 617, 618
Ixodes vespertilionis C. L. Koch 649
Ixodes vestitus Neumann 642
Ixodes sp. 1066, 1162, 1167, 1389

Rhipicephalus evertsi Neumann (3157)
Rhipicephalus haemaphysaloides Supino 584, (3158)
Rhipicephalus muehlensi Zumpt 585
Rhipicephalus sanguineus (Latreille) (586), (587)
Rhipicephalus sp. 1395

Rothschild specimens in the Nuttall collection with type status

NUTTALL No.	ROTHSCHILD No.	
72	916	*Haemaphysalis celebensis* Hoogstraal, Trapido, and Kohls, 1965. *J. Parasit.* **51:** 1001, figs. 1–9.
360	None	*Ixodes nitens* Neumann, 1904. *Archs. Parasit.* **8:** 459.
565	243	*Amblyomma quasicyprium* Robinson, 1926. *Ticks. A Monograph of the Ixodoidea* Pt. 4: 237, fig. 117.
634	159	*Ixodes percavatus rothschildi* Nuttall and Warburton, 1911. *Ticks. A Monograph of the Ixodoidea* Pt. 2: 221.
647	248	*Ixodes loricatus spinosus* Nuttall, 1910. *Parasitology, Cambridge* **3:** 411, fig. 5.
650	203	*Ixodes fecialis* Warburton and Nuttall, 1909. *Parasitology, Cambridge* **2:** 58, figs. 1–2.
669	178	*Haemaphysalis humerosa* Warburton and Nuttall, 1909. *Parasitology, Cambridge* **2:** 60, figs. 4–5.

Rothschild specimens in the Nuttall collection

N72 R916
1 ♀ *Haemaphysalis hystricis* (*Haemaphysalis celebensis* HOLOTYPE)
ex. *Sus celebensis* (*Sus verrucosus celebensis*)
Celebes. No date (Sulawesi 02°00′S, 121°00′E, Indonesia)
Presented as mounted specimen No. 916 which we unmounted 4.I.1915, C. W. [Cecil Warburton] det. 8.I.1915.
Publications: Nuttall & Warburton (1915: 425, 426); Hoogstraal *et al.* (1965*b*: 1001); Hoogstraal *et al.* (1973: 556).

N73 R915
1 ♂ *Amblyomma caelaturum* [This species epithet crossed out and *cyprium* inserted] (*Amblyomma cyprium*)
ex. *Sus celebensis* (*Sus verrucosus* subsp.)
Celebes. No date (Sulawesi 02°00′S, 121°00′E, Indonesia)
Presented as slide No. 915 which was unmounted, being defective 5.I.1915.
3 ♂ *Amblyomma cyprium* mounted as slides, 2 transparent, 1 opaque—see *slides* No. 73 (i) (ii) (iii) (Nos. 917, 919, 920) (3 slides) (L. E. Robinson det. 26.I.1915) redet. 26.III.1919.
Note: The 3 slide-mounted males were missing from the Nuttall collection in 1977.
Publication: Robinson (1926: 236).

N74 R918
1 N *Amblyomma (? caelaturum* Cooper & Robinson) (*Amblyomma* sp.). Unmounted

from slide labelled as off *Sus celebensis* (*Sus verrucosus* subsp.)
Celebes. No date (Sulawesi 02°00′S, 121°00′E, Indonesia
(L. E. Robinson det. 26.I.1915).

N360 None
1 ♀ *Ixodes nitens* COTYPE (*Ixodes nitens* SYNTYPE)
ex. *Mus macleari* (*Rattus macleari*)
Christmas Island, Pacific Ocean (10°39′S, 105°40′E)
(ex. Shipley coll. No. 2)
Publications: Neumann (1904: 460); Nuttall & Warburton (1911: 185).

N523 None
1 ♀ *Ixodes brunneus* (minus hypostome, digits) (*Ixodes frontalis*)
ex. *Passer montanus*
Saint-Genies-de Malgoires (43°57′N, 04°13′E), Gard, France
16.XI.1908 Albert Hugues
Publication: Nuttall & Warburton (1911: 192).

N545 R258
Amblyomma sp. [sex/stage not given] (1 ♀ *Amblyomma geoemydae*) (tentative determination)
Found on ground at Paquil, Luzon, Philippine Islands (locality not verified)
15.I.1895 A. Everett
Publication: Robinson (1926: 48) recorded this as *A. americanum.*

N546 R174
Amblyomma triguttatum [sex/stage not given] (4 ♀ *Amblyomma triguttatum*)
ex. kangaroo
Barrow Island (20°48′S, 115°23′E), N. W. Australia
XI.1900 C. J. T. Tanney. det. L. E. Robinson
Publication: Robinson (1926: 57) indicated ♂'s present but not in Nuttall collection in 1977.

N547 R274
6 ♂, 1 ♀ *Amblyomma australiense*
ex. *Echidna aculeata* (*Tachyglossus aculeatus*)
Mt Anderson (17°58′S, 124°04′E), W. Australia
[No date] C. J. T. Tanney
Publications: Robinson (1926: 135, 136) illustrated ♂ and ♀ from this lot. Taylor (1946: 100) repeated Robinson's descriptions and illustrations.

N549 R254
Hyalomma syriacum [sex/stage not given] (4 ♂ *Hyalomma aegyptium*)
ex. tortoise
No data
Note: An additional 1 ♂, 1 ♀ of this collection sent to New York National Museum, New York City, 18.IV.1913.

N550 R196
Aponomma decorosum [sex/stage not given] (2 ♂ *Aponomma decorosum*)
ex. Australian monitor
Note: *A. decorosum* is found only in Australia and ranges from Queensland south to Victoria.

N552 R179
Amblyomma triguttatum [sex/stage not given] (2 ♂, 3 ♀ *Amblyomma triguttatum*)
ex. kangaroo
Barrow Island (20°48′S, 115°23′E), N. W. Australia
20.XI.1900 C. J. T. Tanney
Publication: Robinson (1926: 57).

N553 R211
Amblyomma triguttatum [sex/stage not given] (4 ♀, 13 N *Amblyomma triguttatum*)
ex. kangaroo
Barrow Island (20°48′S, 115°23′E), N. W. Australia
18.XI.1900 C. J. T. Tanney
Publication: Robinson (1926: 57).

N554 R236
Aponomma exornatum [sex/stage not given] (2 ♂ *Aponomma varanensis*)
ex. *Monitor strix* [name not verified]
? Australia
Note: Collection probably not from Australia. The only collection of *A. varanensis* from Australia is the type ♂ of *A. quadratus* (an inornate form of *A. varenensis*). This single record may have been an accidental importation of tick and host.

N555 R259
Dermacentor rhinocerotis [sex/stage not given] (7 ♂ *Dermacentor rhinocerinus*)
No other data
Note: There is an additional ♂ of this species mounted on a slide.

N556 R287
Aponomma hydrosauri [sex/stage not given] (2 ♂, 1 ♀ *Aponomma hydrosauri*)
? Adelaide (34°55′S, 138°35′E), W. Australia

N557 R198
Amblyomma cajennense [sex/stage not given] (1 ♂, 2 ♀ *Amblyomma cajennense*; 3 ♂ *Amblyomma pecarium*)
ex. peccary *Tayassu* sp.
Santa Andrea, Tabasco
30.V.? '[No particulars]'
Note: The above locality information was taken from the vial label. It should be San Andrés, Estado de Tabasco (18°00′N, 92°40′W), Mexico.

Publication: Robinson (1926: 53) incorrectly gave the Nuttall number as 577.
Amblyomma cajennense is a vector of Wad Medani virus and the rickettsia of Rocky Mountain spotted fever.

N558a R263
1 ♂, 1 ♀ *Hyalomma aegyptium* (*Hyalomma rufipes*)
ex. giraffe, *Giraffa camelopardalis*
No other data
Hyalomma rufipes is the vector of the viruses Dugbe, Tete, Matruh, and Crimean Congo hemorrhagic fever.

N558b R263
2 ♂ *Amblyomma gemma*
ex. giraffe, *Giraffa camelopardalis*
No other data.
Amblyomma gemma is a vector of Nairobi sheep disease virus.

N559 R285
1 ♀ *Amblyomma tholloni*
No host
Mt Ruwenzori (00°23′N, 29°54′E), on the Uganda–Zaire border, Africa 1906 A. F. R. Wollaston

N560 R260
1 ♂ *Amblyomma longirostre*
ex. *Coendou simonsi* (*Coendou bicolor simonsi*)
Charapaya (17°22′S, 66°45′W), Bolivia
22.VI.1901 P. O. Simons
Publication: Robinson (1926: 140).

N561 None
Hyalomma syriacum [sex/stage not given] (4 ♂ *Hyalomma aegyptium*)
ex. Algerian tortoise
N. C. Rothschild

N562 R261
Amblyomma ovale [sex/stage not given] (2 ♂ *Amblyomma ovale*)
ex. *Speothas venaticus*
Charapaya (17°22′S, 66°45′W), Bolivia
27.VI.1901 P. O. Simons

N563 R266
10 ♂ '[small and large]' *Dermacentor rhinocerotis* (7 ♂ *Dermacentor rhinocerinus*)
ex. rhinoceros
No other data
Note: Nuttall, in his notebook containing information on ticks sent to various individuals and institutions, indicated that this collection was from Nyasaland, British Central Africa [Malawi] in 1907. One additional ♂ of this collection was sent to Dr J. G. Parham, Marromeu, Zembezia, Portuguese East Africa [People's Republic of Mozambique], 18.IV.1913 and one additional ♂ was sent to New York National Museum, New York City, 18.IV.1913.

N564 R218
Amblyomma badium [The species epithet crossed out and *sublaeve* inserted] (6 ♂ *Amblyomma compressum*)
ex. white-bellied pangolin, *Manis tricuspis*
No other data
L. E. Robinson det. 1926

N565 R243
1 ♀ *Amblyomma quasicyprium* Robinson, 1926 TYPE (*Amblyomma cyprium*)
ex. Spider monkey *Ateles melanochoerus* [This species epithet is crossed out and *melanochir* inserted] (*Ateles g. geoffroyi*)
Frontera, (18°32′N, 92°38′W), Tabasco, Mexico
Notes: Both host and locality are incorrect for *Amblyomma cyprium* although this ♀ appears to be true *A. cyprium.*
Nuttall 575 and 3330 also bear Rothschild number R243.
Publications: Robinson (1926: 237, 238) incorrectly gave the Nuttall number 564 for this collection. Taylor (1946: 116) repeated Robinson's error for the Nuttall number.

N566 R270
1 ♀ *Amblyomma ovale*
ex. *Speothas venaticus*
Charapaya (17°22′S, 66°45′W), Bolivia
Publication: Robinson (1926: 29) gave the date as 1900 and indicated that the collection contained only males.

N567 R282
Amblyomma albolimbatum [sex/stage not given] (2 ♂, 1 ♀ *Amblyomma albolimbatum*)
ex. *Morelia variegata* (*Morelia spilotes variegata*)
Perth (31°56′S, 115°50′E), W. Australia.
Woodward
L. E. Robinson det. 1926

N568 R231
Amblyomma [species epithet *integrum* crossed out and *dissimile* inserted]: [sex/stage not given] (7 ♂, 2 ♀, 7 N *Amblyomma dissimile*)
ex. large snake
Probably Frontera (18°32′N, 92°38′W), Tabasco, Mexico
May 1. 1.V.1901 [The full date is on vial label but not in catalogue]
Publication: Robinson (1926: 167) indicated the date for this collection was V.1900 and that only one female was present.

N569 R267
Amblyomma moreliae [sex/stage not given] [This species epithet crossed out and *albolimbatum* inserted] (1 ♀ *Amblyomma albolimbatum*)

ex. *Diemenia superciliosa* (*Diemenia textilis*)
Herdman's Lake, near Perth (31°56′S, 115°15′E), W. Australia
Det. Neumann & Warburton
Publication: Robinson (1926: 226) figured this ♀; on p. 227 he incorrectly gave the collection number as N1569.

N570 R182
2 ♂ *Amblyomma marmoreum*
leopard tortoise
[Africa]
No other data
L. E. Robinson det.
Note from Mr. Robinson 17.XI.1922: 'They originally showed the characteristic ornamentation, sufficient of which is still visible, especially if examined under alcohol, to leave no doubt. The coarse punctations are larger than those seen in specimens off Rhinoceros in East Africa, and the dark ornamentation is more salient, but I do not consider these differences to be of specific importance. The other morphological characters are typical.'

N572 R288
Haemaphysalis hystricis [sex/stage not given] (3 ♀ *Haemaphysalis hystricis*)
ex. *Canis familiaris*
Lhassia, Assam, India (coordinates for Assam—26°00′N, 93°00′E)
1907. R. A. Lorrain
Note: Nuttall sent 1 ♂, 1 ♀ of this collection to Dr L. O. Howard of the U.S. Department of Agriculture. These specimens are now deposited in the Rocky Mountain Laboratory collection (RML 109001).
Publications: Nuttall & Warburton (1915: 425); Hoogstraal *et al.* (1965*a*: 476) gave combined collection data from Nuttall 572 and 573.

N573 R293
Haemaphysalis hystricis [sex/stage not given] (2 ♀ *Haemaphysalis hystricis*)
ex. *Canis familiaris*
Lhassia, Assam, India (coordinates for Assam—26°00′N, 93°00′E)
1907. R. A. Lorrain
Publication: Hoogstraal *et al.* (1965*a*: 476) gave combined data from Nuttall 572 and 573.

N574 R294C
Haemaphysalis bispinosa [sex/stage not given] (10 ♂, 6 ♀, 1 N *Haemaphysalis bispinosa*)
No other data
Haemaphysalis bispinosa is a vector of Kyasanur forest disease virus.

N575 R243
♀ *Haemaphysalis hystricis* (2 ♀ *Haemaphysalis hystricis*))
Note: Nuttall 565 and 3330 also bear Rothschild number R243.

N575x R163
Haemaphysalis leachi? [sex/stage not given] (1 ♂ *Haemaphysalis indica*)
ex. *Hyaena crocuta* (*Hyaena hyaena*)
Darie (locality not verified)
(Exp. Erlanger Hilgert)
Note: The Nuttall number for this collection is 575x in his catalogue but 575a on the vial label. Nuttall 1395 also bears Rothschild number R163.

N576 R294a
Haemaphysalis hystricis [sex/stage not given] (1 ♀, 1 N *Haemaphysalis hystricis*)
ex. *Canis familiaris*
Lushai Hills (23°10′N, 92°50′E), Assam, India
1907. R. A. Lorrain
Publications: Nuttall & Warburton (1915: 425) indicated that N576 was composed of 1 ♂, 3 ♀. Hoogstraal *et al.* (1965*a*: 476) saw the ♀ labeled N576ii. The nymph, in a separate vial bears the label N576i.

N577 R294
Haemaphysalis leachi [sex/stage not given] (1 ♂, 1 ♀ *Haemaphysalis leachi*)
ex. *Ictonyx capensis* (*Ictonyx striatus*)
Bulawayo (20°09′S, 28°35′E), Zimbabwe
3.IV.1907 E. C. Chubb
Notes: The genus *Ictonyx* is also known in the literature as *Zorilla.* I. Geoffroy, 1826.
Nuttall 595 also bears Rothschild number R294.
Publication: Nuttall & Warburton (1915: 471).

N578 R154
Haemaphysalis leachi (?) (not long enough) [sex/stage not given] (2 ♂, 1 ♀ *Haemaphysalis leachi*)
Deelfontein (20°17′S, 32°38′E), Zimbabwe
1.IV.1902 C. J. B. Grant
Publication: Nuttall & Warburton (1915: 472) indicated the genus as *Suricata*. However, the collection locality appears to be out of the known range of the meerkat.

N579 R212
Haemaphysalis campanulata [sex/stage not given] (2 ♂, 1 ♀ *Haemaphysalis campanulata*)
ex. *Canis familiaris*
Yokohama (35°26′N, 139°37′E), Japan
24.IV.1902 Allan Owston
Note: Nuttall 609 also bears the Rothschild number R212 but the data do not correspond to N579.
Publication: Nuttall & Warburton (1915: 472) indicated the collection contained 2 ♂, 2 ♀ from a dog.

N580 R160
1 ♂ 1 ♀ *Haemaphysalis punctata*
[no host data]
Cambridge (52°13′N, 00°08′E), England
A. E. Shipley (Nuttall det.)
Haemaphysalis punctata is a vector of the viruses Bhanja, tickborne encephalitis, Crimean Congo hemorrhagic fever, and perhaps Tribec.

N581 R183
1 N *Haemaphysalis spinulosa*? [The species epithet crossed out and sp. inserted] (Probably *H. leachi* var. *indica*) (1 N *Haemaphysalis* sp.) (Bad condition, very queer. C. Warburton)
ex. flying squirrel
Bunguran (possibly Bungura 26°20′N, 84°05′E), India

N582 R284
Haemaphysalis bispinosa [sex/stage not given] (2 ♀ *Haemaphysalis bispinosa*)
ex. *Equus caballus*
Lushai Hills (23°10′N, 92°50′E), Assam, India
26.VI.1907 R. A. Lorrain
Publication: Nuttall & Warburton (1915: 431).

N583 R291
Haemaphysalis bispinosa [sex/stage not given] (1 ♂, 1 ♀ *Haemaphysalis bispinosa*)
ex. *Talpa* sp.
Lushai Hills (23°10′N, 92°50′E), Assam, India
1907 R. A. Lorrain
Publication: Nuttall & Warburton (1915: 431).

N584 R294b
Rhipicephalus haemaphysaloides [sex/stage not given] (3 ♂, 1 ♀ *Rhipicephalus haemaphysaloides*)
No data

N585 R242
Rhipicephalus appendiculatus [sex/stage not given] (2 ♂ *Rhipicephalus muehlensi*)
No data

N588 R255
Boophilus sp. incert. [sex/stage not given] (10 ♀ *Boophilus microplus*)
No host data
Entre-Rios, Argentina. Probably—Provincia de Entra Rios (32°00′S, 59°00′W), Argentina. (There are also two small populated areas with the name Entra Rios at 23°18′S, 64°11′W and 28°50′S, 64°11′W, which could be the collection locality.)
IV.1897 Dr C. Berg [C. Warburton det. 1918]
Note: This collection also contained 1 ♂ of the human sucking louse *Pediculus humanus*.
Boophilus microplus is a vector of the viruses Wad Medani, Seletar, and Crimean Congo hemorrhagic fever.

N589 R290
Argas persicus [sex/stage not given] (9 ♂, 6 ♀, 5 N *Argas persicus*))
No history

N590 R292
Argas persicus [sex/stage not given] (11 ♂, 4 ♀, 11 N *Argas persicus*)
No history
Note: An additional 1 ♂, 1 ♀ of this collection were presented to J. de Meza of Zomba, Malawi, 19.II.1916.

N591 R214
16L *Argas vespertilionis*
ex. bat (also parasites off mouse)
No particulars

N592 R195
3L *Argas vespertilionis* (& *Nycteribia*)
ex. *Scot'us wroughtoni* (*Scotophilus temmincki wroughtoni*)
Helwak (17°22′N, 73°44′E), Maharashtra, India.

N593 R224
Argas vespertilionis [sex/stage not given] (3 L *Argas vespertilionis*)
ex. *Vesperugo pipistrellus* (*Pipistrellus pipistrellus*)
Puttenham (51°49′N, 00°44′W), England
28.VII.1899

N594 R240
Ornithodoros talaje [sex/stage not given] (14 N *Ornithodoros capensis* group)
ex. nestlings
Arrows Sand? Puhekiox, Hawaii (locality not verified)
30.VI.1900 H. W. Henshaw

N597 R153
Ixodes hexagonus [sex/stage not given] (8 N 1 L, *Ixodes hexagonus*)
ex. *Erinaceus europaeus*
Belgium. E. A. Boulenger
Publication: Nuttall & Warburton (1911: 183).
Ixodes hexagonus is a vector of tickborne encephalitis virus.

N598 R206
Ixodes hexagonus [sex/stage not given] (1 ♀, 6 N *Ixodes hexagonus*)
ex. otter (*Lutra vulgaris*) (*Lutra lutra*)
No particulars
Publication: Nuttall & Warburton (1911: 182) indicated that the locality was England.

N599 R209
Ixodes hexagonus [sex/stage not given] (3 ♀, 4 N *Ixodes hexagonus*)
ex. *Erinaceus europaeus*
Cambridge (52°13′N, 00°08′E), England
Publication: Nuttall & Warburton (1911: 182).

N600 R221
Ixodes hexagonus [sex/stage not given] (3 ♀, 1 L *Ixodes hexagonus*)
ex. polecat *Mustela putorius*
Boxworth (52°16′N, 00°02′W), England
30.IV.1901
Publication: Nuttall & Warburton (1911: 182).

N601 R208
Ixodes hexagonus [sex/stage not given] (1 ♀, 41 L *Ixodes hexagonus*)
ex. otter (*Lutra vulgaris*) (*Lutra lutra*)
No other data
Note: One larva (RML 16476) of this collection was donated to the Rocky Mountain Laboratory by P. A. Buxton, London School of Hygiene and Tropical Medicine, in 1940. (See also Nuttall 1159).
Publication: Nuttall & Warburton (1911: 182) indicated that the locality was England.

N602 R222
1 ♀ *Ixodes hexagonus*
ex. *Mustela erminea*
Tring (51°48′N, 00°40′W), England
19.V.1903
Publication: Nuttall & Warburton (1911: 182).

N603 R179a
Ixodes hexagonus [sex/stage not given] (2 ♀, 1 N *Ixodes hexagonus*)
ex. *Mustela erminea*
Wigginton (51°47′N, 00°38′W), England
4.V.1903 Barrett coll.
Publication: Nuttall & Warburton (1911: 182).

N604 R143
Ixodes hexagonus [sex/stage not given] (4 N *Ixodes hexagonus*)
ex. *Mustela vulgaris* (*Mustela nivalis*)
Tring (51°48′N, 00°40′W), England
20.III.1902.
Publication: Nuttall & Warburton (1911: 182).

N605 R164
Ixodes hexagonus [sex/stage not given] (3 ♀ *Ixodes lividus*)
ex. *Cotile riparia* (*Riparia riparia*)
Worsborough Bridge (53°32′N, 01°28′W), England
6.VII.1906 A. Whitaker coll.
Publication: Arthur (1963: 92)
Ixodes lividus is a vector of tickborne encephalitis virus.

N606 R225
♂'s, ♀'s, & larvae *Ixodes hexagonus* (3 ♀, 6 N, 8 L *Ixodes hexagonus*)
ex. polecat (*Mustela putorius*)
Aberystwyth (52°25′N, 04°05′W), Wales
26.XI.1902.
Publication: Nuttall & Warburton (1911: 183) gave the date as 1902.

N607 R201
Ixodes hexagonus [sex/stage not given] (1 N, 7 L *Ixodes hexagonus*)
ex. *Mustela erminea*
Tring (51°48′N, 00°40′W), England
3.IX.1902
Publication: Nuttall & Warburton (1911: 182) indicated that the collection was composed only of nymphs.

N608 R215
Ixodes hexagonus [sex/stage not given] (4 N *Ixodes hexagonus*)
ex. *Erinaceus europaeus*
Durnberg (48°13′N, 11°55′E), Federal Republic of Germany
3.IX.1898
Publication: Nuttall & Warburton (1911: 183) gave the spelling as Dernberg rather than the catalogue spelling of Dermberg.

N609 R212
1 N *Ixodes hexagonus*
ex. polecat (*Mustela putorius*)
Aberystwyth (52°25′N, 04°05′W), Wales
23.XII.1902
Note: Nuttall 579 also bears the Rothschild number R212 but the data do not correspond to N609.
Publication: Nuttall & Warburton (1911: 183) indicated that more than one nymph was in this collection.

N610 R219
N's, larvae *Ixodes hexagonus* (1 N, 15 L *Ixodes hexagonus*)
ex. *Mustela erminea*
Tring (51°48′N, 00°40′W), England
7.V.1902
Publication: Nuttall & Warburton (1911: 182).

N611 R145
1 N, 1 L *Ixodes hexagonus*
ex. *Mustela erminea*
Lyndhurst (50°52′N, 01°34′W), England
20.III.1901 G. Tate
Publication: Nuttall & Warburton (1911: 182) indicated that multiple nymphs and larvae were in this collection.

N612 R180
♀'s, N's *Ixodes hexagonus* (1 ♀, 7 N *Ixodes hexagonus*)
ex. *Mustela erminea*
Inismore (54°18′N, 07°34′W), Ireland
23.III.1902
Publication: Nuttall & Warburton (1911: 182).

N613 R202
♀'s, N's *Ixodes hexagonus* (5 N *Ixodes hexagonus*)
ex. stoat (*Mustela erminea*)
No other data

N617 R177
1 ♀ *Ceratixodes putus* (*Ixodes uriae*)
ex. wild duck
No other data
Publication: Nuttall & Warburton (1911: 261).
Ixodes uriae is a vector of the viruses tickborne encephalitis, Tuleniy, Oceanside, Zaliv Terpenya, Sakhalin, Tillamook, Avalon, Clo-Mor, Taggert, Bauline, Cape Wrath, Nugget, Tindholmur, Mykines, Great Island, Okhotskiy, Yaquina Head, Poovoot, Paramushir, and Runde.

N618 R220
1 ♂, 1 ♀, 2 N *Ceratixodes putus* (*Ixodes uriae*)
British. E. G. Wheler
No particulars

N619 R147
1 ♂, 2 ♀ *Ixodes tenuirostris* (2 ♂, 2 ♀ *Ixodes trianguliceps*)
ex. *Hypudaeus glareolus* (*Clethrionomys glareolus*)
Campfer (46°28′N, 09°48′E), Switzerland
7.VII.1904 [full date on vial label]. K. Jordan.
Publication: Nuttall & Warburton (1911: 248).
Ixodes trianguliceps is a vector of tickborne encephalitis virus.

N621 R204
N's *Ixodes tenuirostris* (1 N *Ixodes trianguliceps*)
ex. *Sorex vulgaris* (*Sorex araneus*)
Bevendean, (50°51′N, 00°05′E), England
VI.1899.
Publication: Nuttall & Warburton (1911: 248), indicated that more than one nymph was in the collection.

N622 R166
♀ *Ixodes tenuirostris* (1 ♀ *Ixodes trianguliceps*)
ex. *Arvicola amphibius* (*Arvicola terrestris*)
Reservoir
6.IV.1892
Publication: Nuttall & Warburton (1911: 248) indicated the collection was from England.

N623 R197
2 ♀ *Ixodes tenuirostris* (*Ixodes trianguliceps*)
ex. *Arvicola agrestis* (*Microtus agrestis*)
Tring (51°48′N, 00°40′W), England
Publication: Nuttall & Warburton (1911: 248).

N624 R149
1 ♀ *Ixodes tenuirostris* (*Ixodes trianguliceps*)
ex. *Arvicola arvalis* (*Microtus arvalis*)
Campfer (46°28′N, 09°48′E), Switzerland
20.VII.1904 K. Jordan
Publication: Nuttall & Warburton (1911: 248).

N625 R148
3 ♀ *Ixodes tenuirostris* (*Ixodes trianguliceps*)
ex. *Arvicola arvalis* (*Microtus arvalis*)
Campfer (46°28′N, 09°48′E), Switzerland
5.VII.1904 K. Jordan
Publication: Nuttall & Warburton (1911: 248).

N626 R226
♂'s, ♀'s *Ixodes scapularis* (4 ♂, 4 ♀ *Ixodes scapularis*)
ex. *Cariacus virginianus* (*Odocoileus virginianus*)
Craven Co. (35°07′N, 77°03′W), North Carolina, U.S.A.
13.XI.1907 '[det. C. Warburton 5.II.1909. Found with N666]'
Publication: Nuttall & Warburton (1911: 158) gave the date of collection as XI.1897. The date 13.XI.1897 is also on the vial label.

N633 R169
N's *Amblyomma* sp. (8 N *Amblyomma* sp.)
ex. *Macropus* sp.
No other data
Note: Nuttall 644 also bears the Rothschild number R169 and gives the additional data: W. Australia 28.VII.1900.

N634 R159
Ixodes percavatus (2 ♀, 2 N *Ixodes rothschildi* TYPES)
ex. Puffin *Fratercula arctica.* Wrongly labelled *Ix. putus* '(Pocock)' on back of label; no particulars. (Sent to Neumann who confirmed the determination II.1909.)
No other data.
Publications: Nuttall & Warburton (1911: 221) described the ♀ and N of *Ixodes percavatus rothschildi.* Zumpt (1952: 17) raised this taxon to specific rank; Arthur (1953: 222–226) independently raised *I. percavatus rothschildi* to specific rank; Arthur (1963: 134) referred to 2 ♀, 3 N in the type lot.
There was (IX.1977) a note in the vial with the words '1 N Missing'.

N637 R213
Ixodes bicornis [sex/stage not given] (11 ♀ *Ixodes boliviensis*)
ex. *Felis concolor*
'[American]' No other data
Publication: Nuttall & Warburton (1911: 187) indicated only one ♀ in the collection.

N638 R276
1 ♂, 1 ♀ *Ixodes loricatus*
ex. *Didelphia* (*Didelphis* sp.)
Sapucay. Foster coll.
Note: Locality is probably Sapucai (25°19′S, 56°55′W), Paraguay, which is in the range of *I. loricatus.* [See also Nuttall 1391].
Publications: Nuttall & Warburton (1911: 269); Cooley & Kohls (1945: 190).

N639 R256
Ixodes loricatus [sex/stage not given] (1 ♂ *Ixodes loricatus*)
ex. 'Piquoti'
No other data

N640 R241
2 ♂, 2 ♀, 2 N *Ixodes loricatus* (2 ♂, 2 ♀ *Ixodes loricatus*)
ex. *Ateles melanochir* (*Ateles g. geoffroyi*)
Frontera (18°32′N, 92°38′W), Tabasco, Mexico. Note following locality '(Compared with Neumann's types at Toulouse, 1910; agrees fully but Nn's type larger).'
Publications: Nuttall & Warburton (1911: 269); Cooley & Kohls (1945: 190).

N641 R161
Ixodes loricatus [sex/stage not given] (2 ♂, 1 L *Ixodes loricatus*)
ex. *Didelphys aurita* (*Didelphis marsupialis*)
Brazil 24.XI.1901
Publications: Nuttall & Warburton (1911: 269); Cooley & Kohls (1945: 190).

N642 R165
1 ♀, 1 N, 6 L *Ixodes vestitus* (1 ♀, 5 N *Ixodes vestitus*)
ex. *Diemenia superciliosa* (*Diemenia textilis*)
Herdman's Lake, near Perth (31°56′S, 115°15′E), W. Australia
B. H. Woodward
Note: Nuttall 628 also bears Rothschild number R165.
Publications: Nuttall & Warburton (1911: 255) indicated larvae as did the catalogue entry. These were missing 7.X.1977. Taylor (1946: 59, 60) repeated Nuttall & Warburton's description and figures. Roberts (1960: 451, 452).

N643 R265
2 N *Ixodes holocyclus*
Perth (31°56′S, 115°15′E), W. Australia
B. H. Woodward coll.
Publication: Nuttall & Warburton (1911: 238).

N645 R275
3 ♀ *Ixodes australiensis*
ex. tame dog (*Canis familiaris*)
Cranbrook (34°18′S, 117°32′E), West Australia
1.IV.1900 J. T. Young
Publications: Nuttall & Warburton (1911: 252). Taylor (1946: 57, 58) repeated Nuttall & Warburton's descriptions and figures.
Note: This collection was seen by R. A. Cooley in 1946 who made 3 slides of dissections (♀ spiracular plate; ♀ legs I & IV; ♀ hypostome) all in the Nuttall collection at the British Museum (N.H.). He gave them the Rocky Mountain Laboratory (RML) number 22284.

N646 R210
Ixodes australiensis [sex/stage not given] (8 ♀ *Ixodes australiensis*)
ex. *Bettongia lescuri* (*Bettongia lesueuri*)
Kojonup (33°50′S, 117°09′E), W. Australia
4.XI.1900
Publications: Nuttall & Warburton (1911: 252). Taylor (1946: 57, 58) repeated Nuttall & Warburton's description and figures. Roberts (1960: 440); Roberts (1970: 40) gave the correct spelling of the locality.

N647 R248
3 ♀ *Ixodes loricatus* var. *spinosus* n. var. Nuttall, 1910 (2 ♀ *Ixodes luciae*)
ex. large opossum (*Didelphis* sp.)
Frontera (18°32′N, 92°38′W), Tabasco, Mexico
May. Found with 648. Note long spine on coxa I.
Note: These are the TYPE SPECIMENS of *I. loricatus spinosus.*
Publications: Nuttall (1910: 411), original description. Nuttall & Warburton (1911: 269), repeated original description and figures.

N648 R248
N's & larvae *Amblyomma ?cajennense* (16 N *Amblyomma cajennense*)
ex. large opossum (*Didelphis* sp.)
Frontera (18°32′N, 92°38′W), Tabasco, Mexico
May
Note: Found with Nuttall 647

N649 R185
1 N *Ixodes vespertilionis.*
ex. *Vespertilio tricolor* (*Myotis tricolor*)
Kei Road, W. Kingwilliamstown, S. Australia [S. Australia crossed out and S. Africa inserted]. Kei Road, King William's Town (32°51′S, 27°22′E), South Africa.
Purchased of Capt. H. Trevelyan.
Publications: Nuttall & Warburton (1911: 277). Taylor (1946: 41) considered *I. vespertilionis* 'very doubtfully Australian' and 'original specimen is unfortunately lost'. Hoogstraal (1956: 569, 570) considered this collection to be of South African origin.
Ixodes vespertilionis is a vector of the viruses Issyk Kul and tickborne encephalitis.

N650 R203
1 ♀ *Ixodes fecialis* TYPE (HOLOTYPE)
ex. *Dasyurus geoffroyi*
Cranbrook (34°18′S, 117°32′E), W. Australia
5.III.1900
Publications: Warburton & Nuttall (1909: 58) original description. Nuttall & Warburton (1911: 248) repeated the original description and figures as did Taylor (1946: 56). Roberts (1960: 445) incorrectly gave the collection date as March 1910.

N652 R168
2 ♀ *Ixodes unicavatus* (1 ♀, 1 N *Ixodes unicavatus*)
ex. shag (*Phalacrocorax aristotelis*)
Plymouth (50°23′N, 04°10′W), England
IX.1897
Publications: Nuttall & Warburton (1911: 266) indicated that the collection consisted of only one nymph. Arthur (1963: 126) repeated this error.

N666 R226
1 ♀ *Dermacentor nigrolineatus* (1 ♀ *Dermacentor albipictus*)
ex. *Cariacus virginianus* (*Odocoileus virginianus*)
Craven Co. (35°07′N, 77°03′W), North Carolina, U.S.A. Found with N626 q.v. for details.
C. Warburton det. 1917
Dermacentor albipictus is a vector of Colorado tick fever virus.

N667 R250
♀'s, N's *Ixodes unicavatus* (3 ♀, 10 N, 3 L *Ixodes unicavatus*)
ex. *Phalacrocorax graculus* (*Phalacrocorax aristotelis*)
Cromarty (57°40′N, 04°02′W), Scotland.
10.III.1898 W. Roy
Publications: Nuttall & Warburton (1911: 266); Arthur (1963: 126).

N669 R178
Haemaphysalis humerosa [sex/stage not given] TYPES (2 ♂, 1 ♀, 1 N *Haemaphysalis humerosa* TYPES)
ex. *Parameles macrura* (*Isoodon macrourus*)
Barrow Island (20°48′S, 115°23′E), N. W. Australia
Note: An additional 1 ♂ of this collection was sent to Dr L. O. Howard, U.S. Dept. of Agriculture, Washington, D.C., U.S.A. 21.V.1909.
Publications: Warburton & Nuttall (1909: 60) original description. Nuttall & Warburton (1915: 496, 497) and Taylor (1946: 82) repeated original description and figures. Roberts (1963: 39) discussed the type series and the note inserted in the tube by Nuttall that one specimen was missing 20.X.1934.

N670 R172
Haemaphysalis elongata [sex/stage not given] (1 ♂ *Haemaphysalis elongata*, 4 ♂, 2 ♀ *Haemaphysalis tiptoni*)
ex. *Centetes ecaudatus* (*Tenerec ecaudatus*)
Madagascar
Note: The male of *H. elongata* has been given a collection number by the Rocky Mountain Laboratory (RML 71004) and by Harry Hoogstraal (HH44251).
Publications: Nuttall & Warburton (1915: 500). Hoogstraal (1953: 59, 64) discussed the two species represented in Nuttall & Warburton's (1915) figures and descriptions.

N826 R189
2 ♀ *Ixodes hexagonus* (*Ixodes rubidus*)
ex. Coypu, *Myopotamus coypus* (*Myocaster coypus*)
S. America. No further particulars
Publication: Nuttall & Warburton (1911: 183).

N892 R295
Haemaphysalis bispinosa [sex/stage not given] (7 ♂, 7 ♀ *Haemaphysalis bispinosa*)
ex. *Canis familiaris*
Luthaia Mts, Assam
Note: The locality is questionable. There are no Luthaia Mts as written in the catalog or Southaia Mts as in Nuttall & Warburton (1915: 431) to be found in gazetteers of India. I believe the locality to be Lushai Hills (23°10′N, 92°50′E), Assam, India as in N576, (R294a) and N582 (R284).
Publication: Nuttall & Warburton (1915: 431).

N1066 R245
5 ♀ *Ixodes texanus* var. (*Ixodes* sp. not *I. texanus* or *I. hearlei*)
No other data

N1067 R200
1 ♀ *Ixodes hexagonus*
ex. fox (*Vulpes vulpes*)
Boxworth (52°16′N, 00°02′W), England
22.I.1898
Publication: Nuttall & Warburton (1911: 182).

N1068 R190
6 ♂, 6 ♀ *Ixodes canisuga* (4 ♂, 4 ♀ *Ixodes lividus*)
Lyndhurst (50°52′N, 01°34′W), England 11.VII.1900
Publications: Nuttall & Warburton (1911: 214). Arthur (1963: 92) indicated 6 ♂, 6 ♀ present. There were 4 ♂, 4 ♀ in the collection as of IX.1977.

N1069 R146
1 ♂, 2 ♀, 3 N *Ixodes tenuirostris* (*Ixodes trianguliceps*)
ex. *Arvicola arvalis* (*Microtus arvalis*)
Campfer (46°28′N, 09°48′E), Switzerland
11.VII.1904 Dr K. Jordan
Publication: Nuttall & Warburton (1911: 248).

N1105 None
3 ♂, 3 ♀, 6 N *Dermacentor albipictus*
Blucher Hall (51°06′N, 120°01′W), British Columbia, Canada
III.1910. Rec'd 2.IV.1910 from Hon. N. C. Rothschild (London).

N1151 R296
10 L *Argas vespertilionis*
ex. *Pipistrellus pipistrellus*
Oristano (39°54′N, 08°35′E), Sardinia
May 1907 Dr A. Krausse

N1152 R175
6 L *Argas vespertilionis*
ex. *Vesperugo pipistrellus* (*Pipistrellus pipistrellus*)
Tring (51°48′N, 00°40′W), England
1.IX.1898

N1153 R244
2 L *Argas vespertilionis*
No other data

N1154 R271
2 L *Argas vespertilionis* (*Argas (Carios)* sp.)
Perth (31°56′S, 115°50′E), W. Australia
Note: These specimens may represent a new species. It is not *Argas australiensis, Argas daviesi* or *Argas dewae*, the currently known representatives of the subgenus *Carios* in Australia.

N1159 R142
N's *Ixodes hexagonus* (3 N *Ixodes hexagonus*)
ex. *Mustela erminea*
Tring (51°48′N, 00°40′W), England
10.IV.1902.
Note: One nymph (RML 16476) of this collection was donated to the Rocky Mountain Laboratory collection by P. A. Buxton, London School of Hygiene and Tropical Medicine, in 1940. (See also Nuttall 601).
Publication: Nuttall & Warburton (1911: 182).

N1160 R194
L's *Ixodes hexagonus* (17 L *Ixodes hexagonus*)
ex. fox *Vulpes vulpes* (cub)
Boxworth (52°16′N, 00°02′W), England
30.III.1900
Note: 2 additional larvae from this collection were sent to Prof. R. Matheson, Cornell University, Ithaca, N.Y., U.S.A., 27.V.1929.
Publication: Nuttall & Warburton (1911: 182).

N1161 R278
♀ *Ixodes tenuirostris* (*Ixodes trianguliceps*)
Tarasp (46°38′N, 10°25′E), Switzerland
summer 1901
Publication: Nuttall & Warburton (1911: 248)

N1162 R207
2 L *Ixodes* sp.
ex. *Dromicia concinna* (*Cercartetus concinnus*)
Note: The nocturnal marsupial *C. concinnus* inhabits the southern part of western and central Australia.

N1163 R247
L's *Argas vespertilionis* (13 L *Argas vespertilionis*)
ex. *Vesperugo pipistrellus* (*Pipistrellus pipistrellus*)
Yalding (51°14′N, 00°26′E), England.
8.VIII.1897 [However, 1997 was written]
W. R. Ogilvie-Grant

N1164 R250, 251
L's *Argas* sp. (5 L *Argas boueti*)
ex. either *Phalacrocorax graculus*, Cromarty, or *Megaderma cor*, Salamana, Havish, 4,500 ft (Number on cork defaced)
ex. *Megaderma cor.*
Salamana, Havish 1,372 m (locality not verified)
Notes: *Megaderma cor* ranges in East Africa from Ethiopia to Tanzania.
The correct Rothschild number for this collection is R251. For R250 see Nuttall 667.

N1166 R230
10 nymphs [genus & species not given] (*Amblyomma* sp.)
ex. *Mus escularis* (name not verified)
St Aignan. Possibly Misima Island (10°41′S, 152°42′E), Louisade Archipelago. This island was formerly known as St Aignan.
VIII-XI. 1897 (Meek)

N1167 R186
N1167a
2 N *Ixodes* sp. [1167], 1 ♂ *Hyalomma aegyptium* [1167a] (*Hyalomma truncatum*)
ex. a 'Sassaby' a bastard hartebeest
(*Damaliscus lunatus*) Republic of South Africa. Date?
Hyalomma truncatum is a vector of the viruses Dugbe, Bhanja, Jos, and Crimean Congo hemorrhagic fever.

N1211 R237
2 N *Ixodes* sp. (2 N, 1 L *Ixodes fecialis*)
ex. *Tarsipes rostratus* or *Smiothopsis murinus* [vial label reads *S. murinus*] (*Sminthopsis murina*)
Albany (35°02′S, 117°53′E), W. Australia
21.XII.1900 B. H. Woodward

N1212 R272
5 N *Ixodes* sp. (*Ixodes holocyclus*)
Perth (31°56′S, 115°50′E), W. Australia
B. H. Woodward
No further details

N1213 R216
1 ♀ *Ixodes fecialis* var. *aegrifossus* (*Ixodes fecialis*)
ex. *Perameles obesula* (*Isoodon obesulus*)
Bannister (32°40′S, 116°33′E), W. Australia
21.VIII.1900
Publication: Nuttall & Warburton (1911: 250).

N1386 R249
N's, L's *Amblyomma* sp. (14 N, 2 L *Amblyomma* sp.)
ex. *Cariacus virginianus mexicanus* (*Odocoileus virginianus*)
San Rafael (20°12′N, 96°51′W), Veracruz, Mexico
27.III.1903

N1387 R264
1 N ? genus (*Dermacentor andersoni*)
ex. *Lagomys princeps* (*Ochotona princeps*)
Canadian National Park, ? Ottawa, Canada
5.VIII.1899 J. F. Dippie
Note: Ottawa, Ontario is far to the east of the ranges of *D. andersoni* and the pika. The Canadian National Park and the date 1899 suggests a relationship to N1390 (R280), Banff National Park, which is within the range of both *O. princeps* and *D. andersoni.*
Dermacentor andersoni is a vector of the viruses Powassan and Colorado tick fever, the bacterium of tularemia, and the rickettsia of Rocky Mountain spotted fever.

N1389 R155
larvae *Ixodes* sp. (3 N *Ixodes* sp.)
ex. *Crysomys longicaudatus* (*Oryzomys longicaudatus*)
Valparaiso (33°02′S, 71°38′W), Chile
Date ? J. A. Wolffshon

N1390 R280
2 N ? genus '(has eyes!)' (2 N *Dermacentor andersoni*)
Banff (51°38′N, 116°22′W), Alberta, Canada
19.VII.1899

N1391 R269
4 N ? genus (3 N *Amblyomma* sp.)
ex. *Didelphys* sp. (*Didelphis* sp.)
Sapucai (25°19′S, 56°55′W), Paraguay
? Date

N1392 R187
N's *Amblyomma* sp. (10 N *Amblyomma* sp.)
ex. Hare wallaby (*Lagorchestes conspicillatus*)
Barrow Island (30°48′S, 115°23′E), N. W. Australia

N1393 R176
larvae *Amblyomma* sp. (64 L *Amblyomma* sp.)
ex. *Bettongia penicillata*
Bokerup, W. Australia. Possibly Bokarup Swamp (34°24′S, 116°50′E).
20.IV.1900

N1394 R227
2 N *Amblyomma* sp.
ex. *Ontalis vetula macalii* (*Neotoma alleni vetula*)
Frontera (18°32′N, 92°38′W), Tabasco, Switzerland [sic.] Mexico
18.V.–

N1395 R163
N's *Rhipicephalus* sp. (2 N *Rhipicephalus* sp.)
ex. *Hyaena crocuta* (*Hyaena hyaena*)
Darie (locality not verified)
? Date. Von Erlanger

N1396 R246
1 N *Amblyomma* sp.
ex. Black squirrel (*Sciurus* sp.)
Frontera (18°32′N, 92°38′W), Tabasco, Mexico
19.V.–

N1397 R171
larvae *Amblyomma* sp. (26 L *Amblyomma* sp.)
ex. *Macropus eugenii* (*Macropus fuligenosus*)
Cranbrook (34°18′S, 117°32′E), W. Australia
6.III.1910

N1398 R150
1 larvae ? genus (1 L *Hyalomma* sp.)
ex. *Gerbillus gerbillus*
Zaghig*
1.III.1903 Hon. N. C. Rothschild
*Locality not verified. However, N. C. Rothschild was in the Nile delta early in 1903. Quite possibly the locality is Zagazig (30°35′N, 31°31′E), Egypt.

N1399 R162b
N's *Ixodes* sp. (4 N, 4 L *Ixodes texanus*)
ex. *Putorius energermanis* (*Mustela vison*)
Sumas, B.C., Canada*
III.1903
*Either Sumas Lake (49°07′N, 122°02′W), British Columbia, Canada or Sumas (49°00′N, 122°13′W), Washington, U.S.A.

N1497 None
1 N *Dermacentor* sp. (*Dermacentor albipictus*)
ex. Moose (*Alces alces*)
New Brunswick, (47°00′N, 66°00′W), Canada
30.XI.1911 J. Birrell coll.

N1498 None
1 ♂ *Dermacentor albipictus*
ex. man (*Homo sapiens*) (Dr Walker)
New Brunswick (47°00′N, 66°00′W), Canada
29.XI.1911 J. Birrell coll.

N1499 None
2 ♂ *Dermacentor albipictus*
ex. Moose (*Alces alces*)
New Brunswick (47°00′N, 66°00′W), Canada
30.XI.1911 J. Birrell coll.

N1500 None
2 ♂, 1 ♀, 1 N *Dermacentor albipictus*
ex. carabou [sic.] (*Rangifer tarandus*)
New Brunswick (47°00′N, 66°00′W), Canada
25.XI.1911 J. Birrell coll.

N1501 None
1 N *Dermacentor* sp. (*Dermacentor albipictus*)
ex. carabou [sic.] (*Rangifer tarandùs*)
New Brunswick (47°00′N, 66°00′W), Canada
25.XI.1911 J. Birrell coll.

N1502 None
1 N *Dermacentor* sp. (*Dermacentor albipictus*)
ex. carabou [sic.] (*Rangifer tarandus*)
New Brunswick (47°00′N, 66°00′W), Canada
25.XI.1911 J. Birrell coll.

N1503 None
1 ♂ *Dermacentor* sp. (5 N *Dermacentor albipictus*)
ex. carabou [sic.] (*Rangifer tarandus*)
New Brunswick (47°00′N, 66°00′W), Canada
25.XI.1911 J. Birrell coll.

N1504 None
1 ♀ *Ixodes hexagonus* (*Ixodes cookei*) '[Not typical—bad condition; possibly *I. rubidus*]'
ex. black cat
New Brunswick (47°00′N, 66°00′W), Canada
19.XII.1911 J. Birrell coll.
Ixodes cookei is a vector of Powassan virus.

N3138 R926
1 ♂ *Aponomma laeve* var. *capensis* (*Aponomma* sp.)
ex. *Echidna* sp.
No further data
Gift of Hon. N. C. Rothschild "(unmounted by me from a slide R926)". L. E. Robinson det.
Note: This is not *Aponomma concolor* or *A. oudemansi.* Coxal spurring is similar to *A. pattoni* but the specimen lacks cervical pits. It is a species near *A. pattoni.*

N3160 R238
2 ♂, 1 ♀, 1 N *Dermacentor reticulatus* (1 ♂, 1 ♀, 1 N *Dermacentor reticulatus*)
Revelstoke, and Revelstoke Point, now known as Stoke Point (50°18′N, 04°01′W), England
III.1902.
Dermacentor reticulatus is a vector of the viruses tickborne encephalitis, Russian spring summer encephalitis, and Omsk hemorrhagic fever.

N3330 R243
1 ♀ *Dermacentor auratus* (*Dermacentor* sp.)
No other data
Note: Nuttall 565 and 575 also bear Rothschild number R243.

N3502 None
♂'s, ♀'s *Dermacentor andersoni* (7 ♂, 9 ♀ *Dermacentor andersoni*)
Okanagan Falls (49°21′N, 119°31′W), British Columbia, Canada
V.1913 Rothschild coll.
Gift of Seymour Hadwen, 1922

N3537 None
N's *Haemaphysalis leachi* (10 N *Haemaphysalis erinacei*)
ex. *Dipodillus campestris* (*Gerbillus campestris*)
Timgad (35°30′N, 06°35′E), Algeria
15.IV.1920 N. C. Rothschild & K. Jordan, coll.
Publication: Hoogstraal (1955: 222, 223) (see note under 3539).

N3538 None
N's *Haemaphysalis leachi* (11 N *Haemaphysalis erinacei*)
ex. *Dipodillus campestris* (*Gerbillus campestris*)
Timgad (35°30′N, 06°35′E), Algeria
15.IV.1920 N. C. Rothschild & K. Jordan coll.

N3539 None
N's *Haemaphysalis leachi* (4 N *Haemaphysalis erinacei*)
ex. *Dipodillus campestris* (*Gerbillus campestris*)
Timgad (35°30′N, 06°35′E), Algeria
17.IV.1920 N. C. Rothschild & K. Jordan coll.
Publication: Hoogstraal (1955: 223) gave the Nuttall number 3739 for this collection. He indicated the total number of nymphs as 17 in combined collections 3537 and 3539. In 1977 the total number of nymphs in these two collections was 14.

A single tick collection given by the Hon. Walter Rothschild to G. H. F. Nuttall via Guy A. K. Marshall

N888 None
2 ♂, 1 ♀ *Hyalomma aegyptium* (*Hyalomma rufipes*)
ex. giraffe (*Giraffa camelopardalis* subsp.)
Ogo, Senegal
ex. Riggenbach coll. given by Hon. Walter Rothschild to African Entomological Committee (rec'd 19.X.1909 from Guy A. K. Marshall).
Notes: There are two populated places and one campsite with the name Ogo in Senegal: PPL. 14°35′N, 15°50′W; PPL. 15°33′N, 13°17′W; CMP. 14°45′N, 15°03′W.
18 specimens of this collection were received 11.X.1909 by the Entomological Research Committee (Anon. 1910).

Rothschild specimens missing from Nuttall collection

N75 R1015, 1017, 1019
3 ♂ *Amblyomma clypeolatum* (= *atrogenatum* N. & W.)
ex. tortoise
Zoological Society's Gardens, London, 11.X.1895
Presented by N. C. Rothschild
Mounted (i) opaque & (ii) (iii) transparent on 3 slides nos. 1015, 1017, 1019
L. E. Robinson det. 26.III.1919

N76 R964
1 ♀ *Amblyomma* sp.
ex Monitor
Kalao Island. No further data
Mounted opaque on slide No. 964 from N. C. Rothschild

N77 R1033, 1034, 1035
3 ♂ *Amblyomma marmoreum*
ex. *Testudo pardalis* (leopard tortoise)
No further data. Mounted as transparent specimens on slides Nos. 1033, 1034, 1035
Presented by N. C. Rothschild
L. E. Robinson det. 26.III.1919

N78 R996, 997, 999
1 ♂, 2 ♀ *Amblyomma albolimbatum*
ex. black & white snake
30.I.1896. No further data. Mounted as transparent specimens Nos. 997, 996, 999
Presented by N. C. Rothschild
L. E. Robinson det. 26.III.1919.

N90 R938–941
4 ♂ *Aponomma gervaisi* var. *lucasi*
ex. *Ophiophagus bungarus* (Hamadryad)
Presented by N. C. Rothschild
No particulars. Mounted on slides 938–941; 2 in glycerine, 2 in balsam
C. Warburton det. I.1915

N91 R900
1 ♂ *Aponomma gervaisi* var. *lucasi*
ex. *Varanus civitatus* (Monitor)
Presented by N. C. Rothschild
No particulars. Mounted as slide 900 in dil. glycerin. C. Warburton det. I.15

N92 R962, 965
2 ♂ *Aponomma gervaisi*
ex. *Varanus civitatus* (Monitor)
Presented by N. C. Rothschild
No particulars. Mounted as slides 962, 965 in glycerin. C. Warburton det. I.1915

N93 R959, 963, 964, 966
4 ♂, 1 ♀ *Amblyomma decoratum*
ex. Monitor
Kalas Island
Presented by N. C. Rothschild
No particulars. 5 slides, 3 in glycerin 2 ♂ in balsam: R959, 961, 963, 964, 966. C. Warburton det. I.1915

N216 R961–973
♀'s, N's, L's *Ixodes hexagonus*
ex. *Lutra vulgaris*
No doubt British
N. C. Rothschild 7 slides

N217 R930, 931
2 ♀ *Ixodes hexagonus*
ex. fox (*Canis vulpes*)
No doubt British
Gift of N. C. Rothschild (2 slides R930–931)

N298 R1000–1011
6 ♀, 5 N, 1 L *Ixodes hexagonus*
ex. stoat (*Putorius erminea*)
No doubt British
Gift of N. C. Rothschild 12 slides

N322 R929
1 ♀ *Ixodes hexagonus*
ex. *Mustela putorius* (ferret)
Probably British
Gift of N. C. Rothschild. R929 mounted in glycerin in glass cell. G. H. F. Nuttall det.

N324 R944–946
3 N *Ixodes hexagonus*
ex. *Erinaceus europaeus*
Probably British
Gift of N. C. Rothschild (3 slides R944–946). G. H. F. Nuttall det.

N395 R988–990
3 L *Ixodes unicavatus* slightly fed
ex. *Phalacrocorax graculus* (shag)
No locality etc. Probably British
Gift of N. C. Rothschild. Mounted on 3 slides R988–90. G. H. F. Nuttall det. 13.II.1915

N396 R1032
1 N *Ixodes brunneus*?
ex. *Erithacus rubecula* (robin)
No data. Probably British
Gift of N. C. Rothschild
Mounted on a slide R1032

N397 R911
1 ♂ *Amblyomma hirtum*
ex. bird (in spirit)
Galapagos Islds, Pacific
Ocean (W. of Ecuador)
Gift of N. C. Rothschild
Mounted on a slide R911. L. E. Robinson det. 6.III.1915

N509 R982, 984–987
4 ♀, 2 N *Ixodes ricinus*
ex. *Cervus capreolus* (roe deer)
? British
Gift of N. C. Rothschild
Mounted on 5 slides R982, 984–987

N516 R901–3, 905
5 N *Ixodes putus*
ex. *Diomedea salvinii* (albatross)
No data
Gift of N. C. Rothschild 5 slides
R901–3, 905

N517 R934
1 ♀ *Ixodes putus*
ex. *Uria lachrymans* (ringed guillemot)

No data
Gift of N. C. Rothschild 1 slide

N518 R975–979
5L *Ixodes putus*
ex. Puffin
No data. Probably British
Gift of N. C. Rothschild 5 slides
G. H. F. Nuttall det. 12.II.1915

N539 R1036
♂ *Haemaphysalis leachi* 1 slide
ex. *Erinaceus albiventris*
Gebel Auli, White Nile, Egypt
9.V.1900 S. & F. Witherby
Received from N. C. Rothschild 1908
Det. G. H. F. Nuttall 27.I.1909

N544 R253
Amblyomma sp. not *varium*; bad condition
ex. 3-toed sloth (*Bradypus tridactylus*)
Brazil

N548 R257
Aponomma gervaisi
ex. Boa
Feb. 1887
Given to D. S. MacLagan 14/10/38

N551 R181
Amblyomma triguttatum
ex. Kangeroo (sic.)
Barrow Island, N. W. Australia
20.XI.1900 C. J. T. Tanney

N571 R279
Aponomma sp.
ex. *Diemenia superciliosa*
Herdman's Lake, Perth, West Australia

N586 R193
♂ *Rhipicephalus sanguineus*
ex. Camel
Locality unknown

N587 R151
2 ♂ *Rhipicephalus sanguineus*
Zaghig, 25.II.1908
N. C. Rothschild coll.

N595 R294
Ornithodoros moubata
No history
Note: Nuttall 577 also bears Rothschild number R294

N596 R157
N's *Ornithodoros megnini*
Okanagan, British Columbia
12.XII.1902 Allan Brooks
Note: *Otobius* is the correct genus for this tick

N620 R942
1 ♀ *Ixodes tenuirostris*
ex. *Mus minutus* (Harvest mouse)
No further particulars '[Mounted on a slide]'

N628 R165
♀ & N *Ixodes ricinus*
No particulars
Note: Nuttall 642 also bears Rothschild number R165

N629 R233
4 ♂ *Ixodes ricinus*
ex. stag
No particulars

N630 R217
3 N *Ixodes ricinus*
ex. *Sciurus vulgaris*
17.IV.1901 Timmer, Ireland

N631 R223
4 ♀ *Ixodes ricinus*
ex. *Erinaceus europaeus*
Belgium E. A. Boulenger coll.

N632 R173
2 ♀ *Ixodes ricinus*
ex. fox
No particulars

N644 R169
2 ♀ *Ixodes holocyclus*
ex. *Macropus* sp.
W. Australia 28.VII.1900
Note: Nuttall 633 also bears Rothschild number R169

N656 R205
2 L *Ixodes ricinus*
ex. *Mustela erminea*
Lyndhurst, Hants., England
25.VII.1900 G. Tate coll.

N674 R922–924
3 ♀ *Ixodes hexagonus*
ex. *Myopotamus coypu*
? locality, host a rodent from S. America
Presented by N. C. Rothschild (R922–924) '[see record of 2 other ♀'s in Ticks Part II, p. 183]'
G. H. F. Nuttall. det. II.1915

N746 R232
larvae *Ixodes hexagonus*
ex. polecat
Aberystwyth, Wales
VIII.1900

N1388 R162
1 L *Argas* sp.
ex. *Putorius energermanis*
Sumas, B.C., Canada
III.1903

N3136 R958
1 ♂ *Hyalomma* sp.

ex. *Capra falconeri* (the Markhoor)
No further data
Gift of N. C. Rothschild (slide R958)
Note: The host occurs in Kashmir, Afghanistan, Gilgit, etc.

N3139 R1012–1020
Hyalomma syriacum
ex. tortoise
No further data
Gift of N. C. Rothschild (5 slides i–v R1012–1020)

N3140 R1022, 1023
2 ♀ *Hyalomma syriacum*
ex. *Testudo pardalis*
No further data
Gift from N. C. Rothschild (2 slides, R1022—1023

N3141 R906, 1031
Hyalomma syriacum
ex. *Araconda* [sic]
No further data (evidently bought slides from M. Pillischer, optician, 88 New Bond St., London W.) Gift of N. C. Rothschild (2 slides R906, 1031)

N3157a R1026–1029
N(3157) 3 ♂ *Rhipicephalus evertsi*
(a) 1 ♂ *Boophilus decoloratus*
ex. Zebra No locality
Gift of N. C. Rothschild 1908
Mounted on slides in balsam (R1026–1029)
R. evertsi det. C. Warburton 18.III.1915
B. decoloratus det. C. Warburton & G. H. F. Nuttall 1915

N3158 R907
1 ♀ *Rhipichephalus haemaphysaloides*
India
Mounted on slide in glycerin
Gift of N. C. Rothschild 1908
(Prep. bought from Fredk. Enock*)
*Spelled Enock in this collection, but see N3159

N3159 R908–910
3 N *Argas reflexus*
India
3 slides, glycerine in cells G. H. F. Nuttall det. III.1915
Gift of N. C. Rothschild 1908
(3 slides Nos. 908–910) Fredk. Enoch prep.
Cost 2 shillings each!

N3351 None
♀ *Amblyomma varium*
ex. *Bradypus tridactylus* (sloth)
Gift of N. C. Rothschild years ago.
Scutum, legs, spiracle on 3 slides
L. E. Robinson det. 26.III.1919

N3536 None
1 ♀ *Argas persicus*
Found on wall
Djama, Algeria
25.II.1920
N. C. Rothschild & K. Jordan coll.

PART II

Rothschild specimens donated to British Museum (Natural History)

Species of Ixodoidea represented in the collection of the British Museum (Natural History), donated by the Hon. N. C. Rothschild

K numbers follow each species. Numbers in parentheses refer to missing collections. Thus, validity of original determinations is unverified.

ARGASIDAE

Argas persicus (Oken) K1, K2, (K148)
Argas reflexus (Fabricius) K3
Argas sanchezi Dugès K4

Ornithodoros talaje Guérin-Méneville K5

IXODIDAE

Amblyomma albolimbatum Neumann K6
Amblyomma americanum (Linnaeus) K7
Amblyomma brasiliense Aragão K8
Amblyomma cajennense (Fabricius) K9
Amblyomma calcaratum Neumann K10
Amblyomma compressum Macalister K11
Amblyomma gemma Dönitz K12, K13, (K149)
Amblyomma humerale C. L. Koch K14, K15
Amblyomma incisum Neumann K16
Amblyomma longirostre (C. L. Koch) K17, K18
Amblyomma maculatum C. L. Koch K19, K20, K21, K22
Amblyomma naponense (Packard) K23
Amblyomma nodosum Neumann K8, K24, K25

Amblyomma ovale C. L. Koch K8, K23, K26, K27, K28, K29, K30, K31, K32
Amblyomma postoculatum Neumann K33
Amblyomma pseudoconcolor Aragão K34
Amblyomma testudinarium C. L. Koch K35
Amblyomma variegatum (Fabricius) K36, K37
Amblyomma sp. K38, K39

Aponomma concolor Neumann K40, K41, K42, K43
Aponomma decorosum (L. Koch) K44, K45, K46, K47
Aponomma exornatum (C. L. Koch) K48
Aponomma fimbriatum (C. L. Koch) K49
Aponomma gervaisi var. *trimaculatus* (Lucas) (K150)
Aponomma latum (C. L. Koch) K50
Aponomma trimaculatum (Lucas) K51

Boophilus decoloratus (C. L. Koch) K52
Boophilus microplus (G. Canestrini) K53
Dermacentor atrosignatus Neumann group K54
Dermacentor reticulatus (Fabricius) K55, K56
Haemaphysalis bancrofti Nuttall and Warburton K57, K58, K59, K60
Haemaphysalis calcarata Neumann K61
Haemaphysalis juxtakochi Cooley K53
Haemaphysalis lagostrophi Roberts K33
Haemaphysalis leachi (Audouin) K62, K63, K64, K66, K67, K68, K69, K70, K71, K72, K73, K74, K75, (K151)
Haemaphysalis leachi indica Warburton (K152)
Haemaphysalis leachi (Audouin) group K76
Haemaphysalis novaeguineae Hirst K77, K78, K79
Haemaphysalis parmata Neumann K80
Haemaphysalis spinigera Neumann K81
Haemaphysalis spinulosa Neumann K82, K83
Haemaphysalis sulcata G. Canestrini, and Fanzago K84, K85
Haemaphysalis tibetensis Hoogstraal K86

Hyalomma aegyptium (Linnaeus) K87
Hyalomma anatolicum excavatum C. L. Koch K88
Hyalomma marginatum C. L. Koch K89
Hyalomma truncatum C. L. Koch K90, (K153)
Hyalomma sp. K91, K92, K93

Ixodes alluaudi Neumann K94, K95, K96, K97, K98
Ixodes cordifer Neumann K99, K100, K101, K102
Ixodes fecialis Warburton and Nuttall K103
Ixodes hexagonus Leach K104, K105, K106, K107, K108, K109, K110
Ixodes loricatus Neumann K111, K112
Ixodes luciae Senevet K113
Ixodes ornithorhynchi Lucas K114
Ixodes cumulatimpunctatus Schulze K115
Ixodes ricinus (Linnaeus) K116, (K154)
Ixodes tasmani Neumann K117
Ixodes thomasae Arthur and Burrow K69
Ixodes trianguliceps Birula K118
Ixodes vespertilionis C. L. Koch K119, K120, K121, K122, K123, K124, (K155)

Rhipicephalus haemaphysaloides Supino K125
Rhipicephalus jeanneli Neumann K126
Rhipicephalus kochi Dönitz K127
Rhipicephalus kochi Dönitz group K128
Rhipicephalus longicoxatus Neumann K127
Rhipicephalus pravus Dönitz K127, K129, K130, K131
Rhipicephalus pulchellus (Gerstäcker) K93, K132
Rhipicephalus sanguineus (Latreille) K133, K134, K135, K136, K137, K138, K139, K140, K141, (K156)
Rhipicephalus simus C. L. Koch K142, K143
Rhipicephalus sp. K144, K145, K146, K147

Rothschild specimens in British Museum (Natural History) collection with type status

B.M.(N.H.) Accession No.	
None	*Dermacentor reticulatus aulicus* Hirst, 1916. *Ann. Mag. nat. Hist.* (8), **17** : 308.
1914.11.17.1–46.	*Haemaphysalis spinigera novaeguineae* Hirst, 1914. *Trans. zool. Soc. Lond.* **20:** 325, fig. 16.
None	*Haemaphysalis tibetensis* Hoogstraal, 1965. *J. Parasit.* **51:** 452, figs. 1–26.

Rothschild specimens in British Museum (Natural History) collection

ARGASIDAE

K1 1912.6.21.21
1 ♂ *Argas persicus*
In railway carriage
El Kantara (35°13′N, 05°43′E), Algeria
17.III.1911
Hon. Walter Rothschild & Ernst Hartert
Argas persicus is a vector of Crimean Congo hemorrhagic fever virus.

K2 1919.8.14.1–70 (pt)
1 ♀ *Argas persicus*
No host
Ouargla house (locality not verified)
E. Hartert and C. Hilgert
Note: The locality is probably a house in Ouargla (31°57′N, 05°20′E), Algeria.

K3 1912.6.21.1–2
1 ♀, 1 N *Argas reflexus*
ex. *Columba livia*
Leipzig (51°18′N, 12°20′E), German Democratic Republic
V.1910
O. Fritsche
Argas reflexus is a vector of the viruses Ponteves and Grand Arbaud.

K4 1912.12.4.1–8
Argas persicus (7 ♂, 5 ♀, 3 N *Argas sanchezi*)
ex. chicken
Price, Pinal Co. (33°05′N, 111°30′W), Arizona, U.S.A.
27.VII.1911
Dr R. E. Kunzr

K5 None
1 ♂, 3 ♀, 3 N *Ornithodoros talaje*
ex. native house
Colombia, S. America

IXODIDAE

K6 1912.6.21.304–318
Amblyomma albolimbatum (19 ♂, 6 ♀ *Amblyomma albolimbatum*; 1 ♀ *Haemaphysalis* sp.; 1 ♀ *Haemaphysalis* sp.)
ex *Trachysaurus rugosus*
Bernier Is. (24°52′S, 113°08′E), W. Australia
1910
B. H. Woodward
Note: 1 ♂, 1 ♀ included in the above total were seen by R. A. Cooley in 1946 who made six slides of dissections (RML 22306).
The *Haemaphysalis* specimens represent either two species or a single exceptionally variable species (Hoogstraal, personal communication).

K7 None
Amblyomma sp. (1 N *Amblyomma americanum*)
ex *Scuirus niger*
Mount Pleasant (32°47′N, 79°52′W), South Carolina, U.S.A.
1909
A. T. Wayne
Amblyomma americanum is a vector of Lone Star virus.

K8 None
Amblyomma nodosum (6 ♂, 1 ♀ *Amblyomma brasiliense*; 25 ♂, 5 ♀ *Amblyomma nodosum*; 1 ♀ *Amblyomma ovale*)
Host unknown
Joinvile (26°18′S, 48°50′W), Humboldt, Estado de Santa Catharina, Brazil
25.VI.1912
W. Ehrhardt

K9 1912.6.21.326–337
6 ♂, 11 ♀, 3 N *Amblyomma cajennense*
ex. cattle, *Canis familiaris* & *Homo sapiens*
St. Ann's (18°21′N, 77°16′W), Jamaica
22–29.III.1911
F. E. Sherlock

K10 None
Amblyomma concolor? '♀ etc.' (7 ♀, 1 N, 4 L *Amblyomma calcaratum*)
ex. *Tapir americanus* (*Tapirus terrestris*)
Joinvile (26°18′S, 48°50′W), Humboldt, Estado de Santa Catarina, Brazil
W. Ehrhardt 15.IX.1912

K11 1912.6.21.299–302
Amblyomma cuneatum (Species epithet crossed out and *compressum* inserted) (1 ♂, 4 ♀ *Amblyomma compressum*)
ex. Pangolin (or Scaly Ant-Eater) *Manis* sp.
Bibianha, Gold Coast. Bebianiha (05°43′N, 00°27′W) or other populated places of this name nearby. Ghana
9.XII.1911
H. G. F. Spurrell
Note: Vial label gives accession number as 1912.6.21.299–303

K12 1911.12.9.1–320 pt
2 ♀ *Amblyomma gemma*
ex. Oxen
Voi (03°23′S, 28°34′E), Kenya
25.IV.1910
Robin Kemp

K13 1911.12.9.1–320 pt
5♂, 4 ♀ *Amblyomma gemma*
ex. Oxen
Voi (03°23′S, 38°34′E), Kenya
30.IV.1910
Robin Kemp

K14 1912.10.31.18–20
1 ♂, 3 ♀ *Amblyomma humerale*
ex. donkey (*Equus asinus*)
Locality unknown

K15 None
4 ♂ *Amblyomma humerale*
ex. turtle
Guyana

K16 None
1 ♂ *Amblyomma incisum*
ex. tapir (*Tapirus* sp.)
Guyana
Note: There is 1 ♀ in this collection which is tentatively being called *A. incisum* but which has a 3/3 hypostome.

K17 1912.6.21.338
1 ♂ *Amblyomma longirostre*
ex. *Galera barbara* (*Eira barbara*)
Mar de Espanha (21°52′S, 43°00′W), Minas Gerais, Brazil
Z. F. Zikan

K18 1912.6.21.339–343
2 ♂, 3 ♀ *Amblyomma longirostre*
ex. *Synetheres prehensilis* (*Coendou prehensilis*)
Mar de Espanha (21°52′S, 43°00′W), Minas Gerais, Brazil
6.III.1911
Z. F. Zikan

K19 1912.10.31.13
1 ♂ *Amblyomma maculatum*
ex. *Canis* sp.
Buenos Aires (34°36′S, 58°27′W), Argentina
30.VI.1912
Miss Idina G. Runnael

K20 1912.12.4.12–14
1 ♂, 1 ♀ *Amblyomma maculatum*
ex. Small Chubut Fox
Bahia Blanca (38°43′S, 62°17′W), Argentina
15.II.1911
E. Weiske

K21 1919.8.14.1–70 pt
4 ♂, 5 ♀ *Amblyomma maculatum*
ex. *Blastocerus dichotomus* (*B. bezoarcticus*)
Parana Delta (vicinity of 33°43′S, 59°15′W), Argentina
25.II.1917
Robin Kemp

K22 None
3 ♂ *Amblyomma maculatum*
ex. *Pseudalopex gymnocerus* (*Dusicyon gymnocerus*)
Laguna Alsina (36°49′S, 62°13′W), to Buenos Aires (34°36′S, 58°27′W), Argentina
V.1916
Robin Kemp

K23 1919.8.14.1–70 pt
Amblyomma mantiquirense (1 ♂ *Amblyomma naponense*)
ex. *Hydrochaerus hydrochaeris*
Eastern Ecuador
This collection also contains 1 ♀ of *Amblyomma ovale* or a closely related species.

K24 None
1 ♂, 1 ♀ *Amblyomma nodosum*
ex. Anteater
Colombia, S. America
1912

K25 1912.6.21.325
1 ♂, 3 N, 3 L *Amblyomma nodosum*
ex. *Myrmecophaga tetradactla* (*Myrmecophaga tridactyla*)
Misantla (19°56′N, 96°50′W), Mexico
I.1911
W. Engelmann
Note: Immature specimens tentatively this sp.

K26 1912.6.21.344–352
8 ♂, 4 ♀, 3 N *Amblyomma ovale*
ex. *Nasua socialis* (*Nasua nasua*)
Mar de Espanha (21°52′S, 43°00′W), Estado de Minas Gerais, Brazil
15.X.1910
Z. F. Zikan
Note: Also present were 1 ♂, 2 ♀ of the mallophagan *Neotrichodectes pallidus*

K27 1912.6.21.353–358
7 ♂, 3 ♀ *Amblyomma ovale*
ex. *Galera barbara* (*Eira barbara*)
Mar de Espanha (20°52′W, 43°00′W), Minas Gerais, Brazil
Z. F. Zikan

K28 1921.12.9.10–11
1 ♂, 1 ♀ *Amblyomma ovale*
ex. *Galictes vittata* (*Grison vittata*)
9.VIII.1916
W. Ehrhardt

K29 1921.12.9.12–20
8 ♂, 2 ♀ *Amblyomma ovale*
ex. *Nasua familiaris* (*Nasua nasua*)
Joinvile (26°18′S, 48°50′W), Humboldt, Estado de Santa Catharina, Brazil
5.VIII.1918
W. Ehrhardt

K30 None
3 ♂, 2 ♀ *Amblyomma ovale*
ex. *Procyon cancrivorus*
Joinvile (26°18′S, 48°50′W), Humboldt, Estado de Santa Catharina, Brazil
24.VII.1912
W. Ehrhardt

K31 None
1 ♂ *Amblyomma ovale*
ex. *Nasua socialis* (*Nasua nasua*)
Mar de Espanha (21°52′S, 43°00′W), Estado de Minas Gerais, Brazil
18.VIII.1911
Z. F. Zikan

K32 None
12 ♂, 5 ♀ *Amblyomma ovale*
ex. *Nasua socialis* (*Nasua nasua*)
Mar de Espanha (21°52′S, 43°00′W), Estado de Minas Gerais, Brazil
18.VIII.1911
Z. F. Zikan

K33 1912.6.21.319–324
Amblyomma albolimbatum (2 ♀ *Amblyomma postoculatum*; 5 ♀ *Haemaphysalis lagostrophi*)
ex. *Lagostrophus fasciatus*
Bernier Island (24°52′S, 113°08′E), W. Australia
1910
B. H. Woodward

K34 None
Amblyomma concolor (2 ♂, 7 N, 3 L *Amblyomma pseudoconcolor*)
ex. Armadillo
La Rioja (29°26′S, 66°15′W), Argentina
E. Giacomelli

K35 1912.12.4.15–16
2 ♂ *Amblyomma testudinarium*
ex. Sheep
Sri Lanka

K36 None
1 N *Amblyomma variegatum*
ex. Raven
Harar (09°19′N, 42°09′E), Ethiopia
17.II.1912
G. Kristensen
Amblyomma variegatum is a vector of the viruses Dugbe, Thogoto, Jos, Crimean Congo hemorrhagic fever, Nairobi sheep disease, Bhanja and Somone.

K37 None
1 ♂ *Amblyomma variegatum*
Host unknown
Harar (09°19′N, 42°09′E), Ethiopia
9.II.1912
G. Kristensen

K38 None
1 N *Amblyomma* sp.
ex. *Canis familiaris*
Harar (09°19′N, 42°09′E), Ethiopia
4.XII.1911
G. Kristensen

K39 None
2 N *Amblyomma* sp.
ex. *Homo sapiens*
Gola National Forest (06°56′N, 10°45′W), Liberia
26.V.1910
R. H. Bunting

K40 1912.6.21.370–380
Amblyomma concolor (3 ♀, 23 N *Aponomma concolor*)
ex. *Echidna aculeata* (*Tachyglossus aculeatus*)
Gippsland District (38°00′S, 147°00′E), Australia
12.IX.1910
A. Coles

K41 None
Amblyomma concolor (11 N *Aponomma concolor*)
ex. *Echidna* sp. (*Tachyglossus aculeatus*)
Australia
A. Coles

K42 1912.6.21.381–383
Amblyomma concolor (3 ♀, 3 N *Aponomma concolor*)
ex. *Echidna aculeata* (*Tachyglossus aculeatus*)
Traralgon (38°12′S, 146°32′E), Australia
29.X.1910
A. Coles

K43 1912.6.21.384–386
Amblyomma concolor (3 ♀ *Aponomma concolor*)
ex. *Echidna* sp. (*Tachyglossus aculeatus*)
Australia
27.II.1911
A. Coles coll.

K44 None
Aponomma decorosum (Species epithet crossed out and *undatum* inserted) (22 ♂, 3 ♀, 3 N *Aponomma decorosum*)
Ex. *Varanus* sp.
Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia
1911
A. Fontaine

K45 1912.6.21.391–401
Aponomma decorosum (Species epithet crossed out and *undatum* inserted) (22 ♂, 6 ♀, 18 N, 2 L *Aponomma decorosum*)
ex. Brown Iguana (*Varanus* sp.)
Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia
A. Fontaine
Publication: Kaufman (1972: 369)

K46 1912.6.21.402–410
Aponomma decorosum (Species epithet crossed out and *undatum* inserted) (15 ♂, 13 ♀, 21 N, 2 L *Aponomma decorosum*)
ex. Black Iguana (*Varanus* sp.)
Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia

A. Fontaine
Publication: Kaufman (1972: 369)

K47 None
Aponomma decorosum (Species epithet crossed out and *undatum* inserted) (1 ♂, 1 ♀, 4 N *Aponomma decorosum*)
ex. Iguana (*Varanus* sp.)
Australia
11.I.1911
Publication: Kaufman (1972: 370)

K48 1912.10.31.21–25
2 ♂ *Aponomma exornatum*
ex. Egyptian monitor (*Varanus* sp.)
Bibianha [Bebaianiha (05°43′N, 00°27′W) or other populated place of this name nearby], Ghanaa
17.XII.1911
H. G. F. Spurrell

K49 1912.6.21.387–390
Aponomma ecinctum (2 ♂, 2 ♀ *Aponomma fimbriatum*)
ex. Tiger snake (*Notechis scutatus*)
Melbourne (37°49′S, 144°58′E), Australia
12.VII.1911
A. Coles
Note: Very poor specimens; hypostomes lacking in all specimens. Capitulum present in only one ♀ but from porose areas and scutal configuration of ♀ and scutum and tarsi of ♂ these appear to be good *A. fimbriatum*.

K50 1912.6.21.416
1 ♂ *Aponomma latum*
ex. *Hystrix* sp.
Mduna River, Hlabisa District, (28°10′S, 32°10′E), Zululand Region, Republic of South Africa
9.III.1910
F. Toppin
Received from Natal Museum, Pietermaritzberg
H. Hoogstraal det. 1952 'unusual host'

K51 1912.6.21.359–369
Aponomma gervaisi var. *trimaculatus* (11 ♂, 2 ♀, 1 N *Aponomma trimaculatum*)
ex. *Python* sp.
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
1911
Prof. F. Forster

K52 None
2 ♀ *Boophilus decoloratus*
Host unknown
Tanzania
Dr E. J. Baxter
Boophilus decoloratus is a vector of the viruses Dugbe, Thogoto, Bhanja, Jos, Somone and Crimean Congo hemorrhagic fever.

K53 1912.10.31.26–29
Haemaphysalis kochi (1 ♀ *Boophilus microplus*; 2 ♂, 1 ♀, 1 N *Haemaphysalis juxtakochi*)
ex. Deer
Caparo (10°27′N, 61°20′W), Trinidad Island, Trinidad and Tobago
22.V.1912
S. M. Klages

K54 1912.12.4.17
1 ♂ *Dermacentor atrosignatus* group
ex. Sheep
Sri Lanka

K55 None
Dermacentor reticulatus var. *aulicus* SYNTYPE (1 ♀ *Dermacentor reticulatus*)
Host unknown
Valescure, nr. St. Raphael (43°26′N, 06°46′E), France
2.IV.1910
Publication: Hirst (1916: 308) original description.

K56 1912.6.21.77–97
2 ♂, 8 ♀ *Dermacentor reticulatus*
ex. *Canis familiaris*
Kuybyshev (55°40′N, 78°12′E), Tomsk, U.S.S.R.
27.VIII.1911
W. M. Thomas

K57 1912.6.21.69–71
1 ♀ *Haemaphysalis bancrofti*
ex. Horse *Equus caballus*
Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia
1911
A. Fontaine

K58 1912.6.21.76
1 ♂ *Haemaphysalis bancrofti*
ex. Black Wallaby [*Macropus dorsalis*, the black-striped wallaby or *Wallabia bicolor*, the black, or black-tailed wallaby, both of which occur in Queensland].
Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia
1911
A. Fontaine

K59 None
2 ♂ *Haemaphysalis bancrofti*
ex. Wallaby (*Wallabia* sp. or *Macropus* sp.)
Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia
1911
A. Fontaine

K60 None
2 ♂ *Haemaphysalis bancrofti*
ex. *Canis familiaris*

Kelsey Creek (20°26′S, 148°27′E), Queensland, Australia
1911
A. Fontaine

K61 None
2 ♂ *Haemaphysalis calcarata*
Host unknown
Voi (03°23′S, 38°34′E), Kenya
14.IV.1910
Robin Kemp

K62 None
Haemaphysalis leachi leachi (2 ♂, 2 ♀ *Haemaphysalis leachi*)
Host unknown
Tanzania
Dr E. J. Baxter

K63 1912.10.31.30–35
Haemaphysalis leachi leachi (9 ♂, 2 ♀ *Haemaphysalis leachi*)
ex. *Felis* sp.
Lake Suai, Ethiopia (locality not verified)
[Hirst original det. *Haemaphysalis* sp.]

K64 1912.6.21.33–35
2 ♂, 2 ♀ *Haemaphysalis leachi*
ex. Hyaena (*Hyaena hyaena*)
Harar (09°19′N, 42°09′E), Ethiopia
31.XII.1911
G. Kristensen

K65 1912.6.21.36–44
10 ♂, 8 ♀ *Haemaphysalis leachi*
ex. *Felis catus*
Harar (09°19′N, 42°09′E), Ethiopia
22.I.1912
G. Kristensen

K66 1912.6.21.45–49
5 ♂ *Haemaphysalis leachi*
ex. Marten
Harar (09°19′N, 42°09′E), Ethiopia
18.I.1912
G. Kristensen

K67 1912.6.21.50–55
5 ♂, 3 ♀ *Haemaphysalis leachi*
ex. 'Badlington' dog
Gola National Forest (06°56′N, 10°45′W), Liberia
17.VI.1910
R. H. Bunting

K68 1912.6.21.56–58
1 ♂, 2 ♀ *Haemaphysalis leachi*
ex. *Felis serval*
Mpwapwa (06°21′S, 36°29′E), Tanzania
15.X.1911
Marschner. Rec'd. from W. Fasius

K69 None
Haemaphysalis leachi (4 ♂ *Haemaphysalis leachi*; 2 ♀ *Ixodes thomasae*)
Host unknown
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
7.VI.1910
Robin Kemp

K70 None
7 ♂, 10 ♀ *Haemaphysalis leachi*
Host unknown
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
6.VI.1910
Robin Kemp

K71 None
4 ♂, 4 ♀ *Haemaphysalis leachi*
Host unknown
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
8.VI.1910
Robin Kemp

K72 None
2 ♂ *Haemaphysalis leachi*
ex. Domestic Rabbit (*Oryctolagus* sp. probably.) The genus *Oryctolagus* does not exist south of the Sahara unless bred in captivity.
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
20.VI.1910
Robin Kemp

K73 None
11 ♂, 8 ♀, 1 N *Haemaphysalis leachi*
Host unknown
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
11.VI.1910
Robin Kemp

K74 None
25 ♂, 11 ♀ *Haemaphysalis leachi*
Host unknown
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
9.VI.1910
Robin Kemp

K75 None
1 ♂ *Haemaphysalis leachi*
ex. *Genetta stuhlmanni*
Fennek, Mutoragwa
Aberdare Mts, Kenya (locality not verified*)
23.III.1910
Robin Kemp
*There is a Mutarakwa Hill (00°47′S, 35°14′E) in the Aberdares that is a possible locality for this collection.

K76 1912.6.21.59–65
Haemaphysalis leachi? (7 ♂, 4 ♀ *Haemaphysalis leachi* group)
ex. *Paradoxurus niger* (*Paradoxurus hermaphroditus*)
Hoshangabad District (22°35′N, 77°40′E), India
1912
C. A. Crump
Received from Bombay Nat. Hist. Soc.

K77 1914.11.17.16–35
Haemaphysalis spinigera var. *novae-guineae* TYPE (19 ♂, 4 ♀, 1 N *Haemaphysalis novaeguineae* paralectotypes)
ex. Kangaroo
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
1911
Prof. F. Forster
Publications: Hirst (1914: 328), original description; Nuttall & Warburton (1915: 452); Roberts (1963: 57)

K78 1914.11.17.1–15
Haemaphysalis spinigera var. *novae-guineae* TYPE (1 ♂ *Haemaphysalis novaeguineae* lectotype; 9 ♂, 11 ♀ *Haemaphysalis novaeguineae* paralectotypes)
ex. *Perameles* sp. ?
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
Prof. F. Forster
Publications: Hirst (1914: 328) original description; Nuttall & Warburton (1915: 452); Roberts (1963: 57) selected lectotype and paralectotypes.

K79 1914.11.17.36–46
Haemaphysalis spinigera var. *novae-guineae* TYPE (6 ♂, 10 ♀, 1 N *Haemaphysalis novaeguineae* paralectotypes)
ex. *Hydromys* sp.
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
1911
Prof. F. Forster
Publications: Hirst (1914: 328), original description; Nuttall & Warburton (1915: 452); Roberts (1963: 57) designated paralectotypes.

K80 1912.6.21.66
1 ♂ *Haemaphysalis parmata*
ex. *Neotragus pygmaeus*
Bebaianiha (05°43′N, 00°27′W) or other populated places of this name nearby, Ghana
10.XI.1911
H. G. F. Spurrell

K81 None
13 N *Haemaphysalis spinigera*
ex. *Lepus* sp.
Hoshangabad District (22°35′S, 77°40′E), India
1912
C. A. Crump
Received from Bombay Nat. Hist. Soc.
Haemaphysalis spinigera is a vector of the viruses Kaisodi and Kyasanur forest disease.

K82 1912.10.31.36–46
Haemaphysalis sp. (28 ♂, 7 ♀ *Haemaphysalis spinulosa*)
ex. Wild cat
Harar (09°19′N, 42°09′E), Ethiopia
6.II.1912
G. Kristensen

K83 None
Haemaphysalis leachi? (1 ♀ *Haemaphysalis spinulosa*)
ex. *Canis familiaris*
Himo River (03°33′S, 37°30′E), Tanzania
30.V.1910
Robin Kemp

K84 1912.6.21.22–32 pt
Haemaphysalis cinnabarina var. *punctata* (2 ♂, 3 ♀ *Haemaphysalis sulcata*)
ex. Sheep
Larnaca (34°55′N, 33°38′E), Cyprus
XI.1911
C. B. Horsbrugh

K85 1912.6.21.22–32 pt
2 ♂, 3 ♀ *Haemaphysalis sulcata*
ex. Sheep
Larnaca (34°55′N, 33°38′E), Cyprus
XI.1911
C. B. Horsbrugh
Note: A portion of this collection was originally entered under *Haemaphysalis cinnabarina* var. *punctata*.

K86 None
Haemaphysalis warburtoni? (1 ♂, 2 ♀, 2 N *Haemaphysalis tibetensis* TYPES
1 ♂ (holotype) 2 ♀, 2 N (paratypes)
ex. *Canis familiaris*
Yatung (27°25′N, 89°00′E) (ca. 3896 m) mouth of Chumbi Valley, Tibet
D. Macdonald
Publication: Hoogstraal (1965: 452), original description.

K87 1912.6.21.247–250
Hyalomma syriacum (3 ♂, 1 ♀ *Hyalomma aegyptium*)
ex. *Testudo graeca ibera*
Hammam Rirha (36°26′N, 02°28′E), Algeria
24.V.1911
Hon. Walter Rothschild & Ernst Hartert

K88 1912.6.21.251–253
Hyalomma syriacum (Species epithet crossed out and *aegyptium* inserted) (4 ♀ *Hyalomma anatolicum excavatum*)
Host unknown
North West Morocco
Received from Hon. W. Rothschild

K89 1912.6.21.240–6
Hyalomma aegyptium (2 ♂, 1 ♀ *Hyalomma marginatum*)
Host unknown
Hammam Rirha (36°26′N, 02°28′E), Algeria
1911
C. Hilgert
Hyalomma marginatum is a vector of the viruses Dhori, West Nile, tickborne encephalitis, Bhanja, Crimean Congo hemorrhagic fever, Tamdy and Batken.

K90 1911.12.9.1–320 (pt)
Hyalomma aegyptium (2 ♀ *Hyalomma truncatum*)
ex. Aged donkey (*Equus asinus*)
Voi (03°23′S, 38°34′E), Kenya
29.IV.1910
Robin Kemp

K91 None
8 N *Hyalomma* sp.
Host unknown
Biskra (34°50′N, 05°40′E), Algeria
25.III.1909
Hon. L. W. Rothschild

K92 1919.8.14.1–70 (part)
3 N *Hyalomma* sp.
ex.? *Dipodillus* (gerbil) (*Gerbillus* (*Dipodillus*) sp.) ('host similar to 108')
Guelt-es-Stel (35°09′N, 03°02′E), Algeria
IV.1912
Hon. Walter Rothschild and Karl Jordan

K93 1912.6.21.202
Rhipicephalus sp. (4 N *Hyalomma* sp.; 1 ♀ *Rhipicephalus pulchellus*; 10 N *Rhipicephalus* sp.
ex. *Lepus* sp.
Harar (09°19′N, 42°09′E), Ethiopia
9.I.1912
G. Kristensen
Rhipicephalus pulchellus is a vector of the viruses Dugbe, Crimean Congo hemorrhagic fever, and Nairobi sheep disease.

K94 None
Ixodes var. of *fecialis* (2 ♀ *Ixodes alluaudi*)
ex. *Lophuromys flavopunctatus zena*
Aberdare Mts (00°25′S, 36°38′E), Kenya
14.II.1910
Robin Kemp

K95 None
Ixodes var. of *fecialis* (1 ♀ *Ixodes alluaudi*)
ex. *Lophuromys flavopunctatus zena*
Aberdare Mts (00°25′S, 36°38′E), Kenya 11,000 ft (3,353 m)
21.II.1910
Robin Kemp

K96 None
Ixodes tenuirostris (2 ♀ *Ixodes alluaudi*)
ex. *Otomys tropicalis elgonis*
Mt Ilkinangop (00°38′S, 36°42′E), Aberdare Mts, Kenya
24.II.1910
Robin Kemp

K97 None
Ixodes tenuirostris (1 ♀ *Ixodes alluaudi*)
Host unknown
Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
15.IV.1910
Robin Kemp
Note: This ♀ has been previously pinned.

K98 None
[undetermined genus & species] (1 N *Ixodes alluaudi*)
ex. *Mus jacksoni* (Possibly *Anomalurus derbianus jacksoni*)
Mutaragwa, Aberdare Mts (locality not verified*), Kenya
13.III.1910
R. Kemp
*There is a Mutarakua Hill (00°47′S, 35°14′E) in the Aberdares that is a possible locality for this collection.

K99 1912.6.21.280–2
4 ♀ *Ixodes cordifer*
ex. *Pseudoircornia* (probably *Pseudocheirus* sp.)
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
1911
Prof. F. Forster

K100 1912.6.21.283
1 ♀ *Ixodes cordifer*
ex. *Dactylopsida trivirgata*
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
Prof. F. Forster
Note: label in vial—seen by Prof. R. A. Cooley 1946. 3 slides of dissections (RML 22285).

K101 1912.6.21.284–8
4 ♀ *Ixodes cordifer*
ex. *Phalanger maculatus*
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
1911
Prof. F. Forster

K102 1912.6.21.279
1 ♂ *Ixodes cordifer*
ex. *Perameles* sp.
Sattelberg, Huon Gulf (07°10′S, 147°25′E), Papua New Guinea
1911
Prof. F. Forster

K103 1912.12.4.11
1 ♀, 4 N *Ixodes fecialis*
ex. *Felis* sp.
Studley Park, Melbourne (37°49′S, 144°58′E), Australia
19.V.1911
A. Coles
Note: Reverse of the vial label bears the inscription—Native cat.

K104 1912.6.21.254—6
5 ♀, 2 N *Ixodes hexagonus*
ex. *Mustela vulgaris* (*Mustela nivalis*)
Tring (51°47′N, 00°39′W), England
12.III.1912
J. F. Cox

K105 1912.6.21.259–61
1 ♀, 2 N, 7 L *Ixodes hexagonus* (1 ♀, 2 N *Ixodes hexagonus*)
ex. *Mustela erminea*
Tring (51°47′N, 00°39′W), England
III.1912
J. F. Cox

K106 1912.6.21.262–3
4 N *Ixodes hexagonus* (4 N, 8 L *Ixodes hexagonus*)
ex. *Meles taxus* (*Meles meles*)
Senj (45°00′N, 14°54′E), Yugoslavia
5.XII.1911
F. Dobiasch

K107 None
22 N, 6 L *Ixodes hexagonus*
ex. *Mustela erminea*
Loch Tay (56°28′N, 04°18′W), Lawes, Scotland
2.III.1911
L. G. Esson

K108 None
1 ♀ *Ixodes hexagonus*
Host unknown
Faugères*, S. France
8.X.1913
W. Davy
N. C. Rothschild
*Three possible localities for Faugères, France: 43°34′N, 03°11′E; 44°28′N, 03°58′E; 44°58′N, 04°35′E.

K109 None
2 N *Ixodes hexagonus*
ex. *Mustela putorius*
Carmarthen (51°52′N, 04°18′W), Wales
1914
F. W. Frohawk

K110 1919.8.14.1–70 (part)
1 ♀ *Ixodes hexagonus*
ex. dog *Canis familiaris*
Bridgnorth (52°32′N, 02°25′W), England
28.X.1916
Miss Frances Pitt

K111 1912.12.4.9–10
1 ♂, 1 ♀ *Ixodes loricatus*
ex. *Didelphis marsupialis aurita*
Mar de Espanha (20°52′S, 43°00′W), Estado de Minas Gerais, Brazil
6.X.1910
Z. F. Zikan

K112 1919.8.14.1–70 pt
2 ♂, 5 ♀ *Ixodes loricatus*
ex. *Lutreolina crassicaudata*
Parana Delta (vicinity of 33°43′S, 59°15′W), Argentina
X.1916
Robin Kemp

K113 1912.6.21.289–292
Ixodes loricatus var. *spinosus* (4 ♂ *Ixodes luciae*)
ex. *Didelphis marsupialis*
San Esteban (11°28′N, 69°22′W), Venezuela
31.I.1911

K114 None
4 ♀, 15 N, 1 L *Ixodes ornithorhynchi*
ex. *Ornithorhynchus paradoxus* (*Ornithorhynchus anatinus*)
Tyalgum Tereed River, perhaps Tyalgum Creek (28°22′S, 153°13′E), New South Wales, Australia
IX.1912
Received from W. F. H. Rosenberg

K115 1912.6.21.272–3
Ixodes rasus (2 ♀ *Ixodes cumulatimpunctatus*)
ex. *Cricetomys gambianus*
Bibianiha (05°43′N, 00°27′W) or other populated places of this name nearby, Ghana
23.XII.1911
H. G. F. Spurrell

K116 1912.6.21.264
3 ♀ *Ixodes ricinus* (2 ♀ *Ixodes ricinus*)
ex. *Canis familiaris*
Porlock Weir (51°12′N, 03°40′W), England
27.IV.1912
F. J. Cox
Ixodes ricinus is a vector of the viruses Tettnang, Tribec, Louping ill, tickborne encephalitis, West Nile, Crimean Congo hemorrhagic fever, Lipovnic, Uukuniemi, Sumakh, Eyack and Kharagysh.

K117 None
Ixodes tasmani? (2 ♂, 1 ♀, 1 N *Ixodes tasmani*)
ex. Nest of *Pseudochirus cooki* (*Pseudocheirus peregrinus*)
N. W. Coast, Tasmania, Australia
IX.1912
R. N. Atkinson

K118 1912.10.31.7–10
Ixodes tenuirostris (1 ♂, 2 ♀, 3 N *Ixodes trianguliceps*)
ex. *Microtus glareolus* (*Clethrionomys glareolus*)
Braunton (51°06′N, 04°11′W), England
21.VI.1912
W. Holland

K119 1912.6.21.267
1 N *Ixodes vespertilionis*
ex. *Rhinolophus ferrumequinum*
Cave de Meaunes, Southern France (locality not verified)
20.I.1908
Dr K. Jordan

K120 1912.6.21.268–9
4 N, 1 L *Ixodes vespertilionis*
ex. Bat?
Monchique (37°20′N, 08°29′W), Portugal
12.V.1910
Dr K. Jordan

K121 1912.10.31.11
1 ♀ *Ixodes vespertilionis*
ex. *Rhinolophus ferrumequinum*
Braunton (51°06′N, 04°11′W), England
22.V.1912
W. Holland
N. C. Rothschild
Note: This ♀ is in alcohol but there is a pin through the idiosoma.

K122 1912.6.21.266
2 N *Ixodes vespertilionis*
ex. *Rhinolophus ferrumequinum*
St Genes de Malgoires (Saint-Genies-de-Malgoires) (43°57′N, 04°13′E), France
IV.1910
Albert Hugues

K123 None
1 N *Ixodes vespertilionis*
ex. bat
Oumasch, Algeria (locality not verified)
5.III.1911
Hon. Walter Rothschild & Ernst Hartert
Note: Theodor (1967: 94) cited a collection of 2 ♂, 3 ♀ *Nycteribia schmidlii schmidlii* off *Plecotus auritus christiei*, Oumasch near Biskra, Algeria, 5.III.1911, Hon. W. Rothschild and E. Hartert. Quite probably this bat was host for both species of ectoparasite.

K124 1912.6.21.270
1 ♀ *Ixodes vespertilionis*
ex. *Rhinolophus hipposideros*
Uj-Moldova (44°44′N, 21°42′E), Romania
1.V.1910
Lintia Dionisius

K125 None
9 N, 5 L *Rhipicephalus h. haemaphysaloides* (4 N, 2 L *Rhipicephalus haemaphysaloides*)
ex. *Lepus* sp.
Hoshangabad (22°46′N, 77°45′W), India
1912
C. A. Crump
Received from Bombay Nat. Hist. Soc.

K126 1912.6.21.203–204
Rhipicephalus kochi (1 ♂ *Rhipicephalus jeanneli*)
ex. grass in tent
Voi (03°23′S, 38°24′E), Kenya
R. Kemp
19.IV.1910

K127 None
Rhipicephalus sp. (3 ♂ *Rhipicephalus kochi*; 1 ♂ *Rhipicephalus longicoxatus*; 6 ♂, 1 ♀ *Rhipicephalus pravus*)
ex. Aged donkey (*Equus asinus*)
Voi (03°23′S, 38°34′E), Kenya
29.IV.1910
Robin Kemp
Rhipicephalus pravus is a vector of Kadam virus.

K128 1912.6.21.239
Rhipicephalus sp. (1 ♀ *Rhipicephalus kochi* group)
ex. Ox
Curepipe (20°19′S, 57°31′E), Mauritius
3.XI.1911
C. Brishoe
Note: Tentative identification: Engorged misshapen specimen.

K129 None
1 ♂, 1 ♀, 10 N *Rhipicephalus pravus*
Host unknown
Taveta (03°25′S, 37°43′E), Kenya
27.V.1910
Robin Kemp

K130 1953.10.9.17
1 ♂ *Rhipicephalus pravus* (1 ♂, 1 N *Rhipicephalus pravus*)
ex. Jerboa? (*Jaculus* sp. ?)
Voi (03°23′S, 38°34′E), Kenya
22.IV.1910
Robin Kemp

K131 1911.12.9.1–320 (part)
Rhipicephalus sp. (25 ♂, 27 ♀ *Rhipicephalus pravus*)
Host unknown

Rombo, Kilimanjaro (03°05′S, 37°20′E), Tanzania
15.VI.1910
Robin Kemp

K132 1912.6.21.229
1 ♂, 1 ♀ *Rhipicephalus pulchellus*
ex. *Homo sapiens* off ground in tent
Nairobi (01°17′S, 36°49′E), Kenya
25.IV.1910
Robin Kemp

K133 1919.8.14.1–70 pt
Rhipicephalus simus (1 ♂, 1 ♀ *Rhipicephalus sanguineus*)
ex. *Vulpes vulgaris* (*Vulpes vulpes*)
Toscana (43°25′N, 11°00′E), Italy
1917
N. Cimballi
Rhipicephalus sanguineus is a vector of Wad Medani virus and the rickettsia of boutonneuse fever.

K134 1919.8.14.1–70 pt
Rhipicephalus simus (1 ♀ *Rhipicephalus sanguineus*)
Host unknown
Firenze (43°46′N, 11°15′E), Italy
N. Cimballi

K135 1912.12.4.18
Rhipicentor (1 ♀ *Rhipicephalus sanguineus*)
ex. dog (*Canis familiaris*)
Livingstone (12°20′S, 30°18′E), Zambia
1912
A. Douglas

K136 1912.6.21.231–232
2 ♀ *Rhipicephalus sanguineus*
ex. *Canis familiaris*
Dehra Dun (30°19′N, 78°04′W), India
1910
Mrs R. Parson

K137 1912.6.21.234–38
6 ♂, 14 ♀ 1 N *Rhipicephalus sanguineus*
ex. *Canis familiaris*
Manaus (03°10′S, 60°00′W), Brazil
1911
Rev. A. Miles Moss

K138 None
Rhipicephalus sp. (1 ♀ *Rhipicephalus sanguineus*)
ex. *Gerbillus indicus* (*Gerbillus* sp.)
Khandala (18°55′N, 73°25′E), India
11.V.1912
J. Assmuth
Note: Tentative identification: Teneral runt female.

K139 1912.6.21.205–220
Rhipicephalus sp. (17 ♂, 6 ♀ *Rhipicephalus sanguineus*)
ex. *Lepus* sp.
Mountains near Droh (34°52′N, 05°53′E), Algeria
8.III.1911
Hon. Walter Rothschild & Ernst Hartert

K140 1912.6.21.201
Rhipicephalus sp. (1 ♀ *Rhipicephalus sanguineus*)
ex. *Erinaceus europaeus*
Saint-Genies-de-Malgoires (43°57′N, 04°13′E), France
21.III.1909
A. Hugues

K141 1919.8.14.1–70 part
Rhipicephalus sp. (2 ♀ *Rhipicephalus sanguineus*)
ex. hedgehog
Hammam Meskoutine (36°27′N, 07°16′E), Algeria
6.V.1914
Hon. Walter Rothschild & Karl Jordan

K142 1912.6.21.230
Rhipicephalus sp. (1 ♂ *Rhipicephalus simus*)
ex. Vulture
Mduna River, Hlabisa District (28°10′S, 32°10′E), Zululand Region, Republic of South Africa
27.III.1910
F. Toppin
Received from Natal Museum, Pietermaritzberg
Rhipicephalus simus is a vector of the viruses Thogoto and Nairobi sheep disease.

K143 None
1 ♂, 5 ♀ *Rhipicephalus simus*
Host unknown
Tanzania
Dr E. J. Baxter

K144 None
1 N *Rhipicephalus* sp.
Host unknown
Biskra (34°50′N, 05°40′E), Algeria
25.III.1909

K145 None
2 N *Rhipicephalus* sp.
ex. *Elephantulus rufescens*
Voi (03°23′S, 38°34′E), Kenya
18.IV.1910
Robin Kemp

K146 None
10 N, 2 L *Rhipicephalus* sp.
ex. *Elephantulus rufescens*
Voi (03°23′S, 38°34′E), Kenya
19.IV.1910
Robin Kemp

K147 None
2 N *Rhipicephalus* sp.
ex. *Elephantulus rufescens*
Voi (03°23′S, 38°34′E), Kenya
25.IV.1910
Robin Kemp

Rothschild specimens missing from British Museum (Natural History) collection

K148 1912.6.21.3–20
Argas persicus
ex. fowls
Larnaca, Cyprus

K149 1911.12.9.1–320 pt
Amblyomma gemma
Host unknown
Kilimanjaro, Brit. E. Africa

K150 1912.6.21.411–415
Aponomma gervaisi var. *trimaculatus*
ex. Iguana
Kelsey Creek, N. Queensland

K151 1919.8.14.1–70 (pt)
Haemaphysalis leachi
ex. Hedgehog
Meskoutine Hamman, Mespot.

K152 1912.10.31.36–46
Haemaphysalis leachi indica
ex. Wildcat
Harar, Abyssinia

K153 1911.12.9.1–320 pt.
Hyalomma truncatum
ex. Donkey
British East Africa

K154 1912.6.21.265
1 ♀ *Ixodes ricinus*
Host unknown
Hamman Rirha, Algeria

K155 1919.8.14.1–70 pt.
Ixodes vespertilionis
ex. *Vespertilio euryalis*
Algeria

K156 1912.6.21.188–200
Rhipicephalus sanguineus
ex. *Erinaceus europaeus*
Montchique [= Monchique], Portugal

Locality list for ticks in the Rothschild collection

N = Nuttall, K = British Museum (Natural History) collections. Numbers in parentheses indicate missing collections.

Abyssinia (K152)
Algeria N561, N3537, N3538, N3539, (N3536), K1, K2, K87, K89, K91, K92, K123, K139, K141, K144, (K151), (K154), (K155)
Argentina N588, K19, K20, K21, K22, K34, K112
Australia N546, N547, N550, N552, N553, N556, N567, N569, N633, N642, N643, N645, N646, N650, N669, N1162, N1211, N1212, N1213, N1392, N1393, N1397, (N551), (N571), (N644), K6, K33, K40, K41, K42, K43, K44, K45, K46, K47, K49, K57, K58, K59, K60, K103, K114, K117, (K150)

Belgium N597, (N631)
Bolivia N560, N562, N566
Brazil N641, (N544), K8, K10, K17, K18, K26, K27, K28, K29, K30, K31, K32, K111, K137
British East Africa (K149), (K153)

Canada N1105, N1387, N1390, N1399, N1497, N1498, N1499, N1500, N1501, N1502, N1503, N1504, N3502, (N596), (N1388)
Chile N1389
Christmas Island, N360
Colombia K5, K24
Cyprus K84, K85, (K148)

Ecuador K23
Egypt (N539)
England N580, N593, N598, N599, N600, N601, N602, N603, N604, N605, N607, N610, N611, N618, N621, N622, N623, N652, N1067, N1068, N1152, N1159, N1160, N1163, N3160, (N216), (N217), (N298), (N322), (N324), (N395), (N396), (N509), (N518), (N656), K104, K105, K110, K116, K118, K121
Ethiopia K36, K37, K38, K63, K64, K65, K66, K82, K93

France N523, K55, K108, K119, K122, K140

Galapagos Islands N397
Germany, Democratic Republic of K3
Germany, Federal Republic of N608
Ghana K11, K48, K80, K115
Guyana K15, K16

India N572, N573, N576, N581, N582, N583, N592, N892, (N3158), (N3159), K76, K81, K125, K136, K138
Indonesia N72, N73, N74
Ireland N612, (N630)
Italy K133, K134

Jamaica K9
Japan N579

Kalao Island (N76)
Kalas Island (N93)
Kenya K12, K13, K61, K75, K90, K94, K95, K96, K98, K126, K127, K128, K129, K130, K132, K145, K146, K147

Liberia K39, K67
Louisade Archipelago N1166

Madagascar, Democratic Republic of N670
Malawi N563
Mauritius K127
Mexico N557, N568, N640, N647, N648, N1386, N1394, N1396, K25
Morocco K88

Papua New Guinea K51, K77, K78, K79, K99, K100, K101, K102
Paraguay N1391
Philippine Islands N545
Portugal K120, (K156)

Romania K125

Sardinia N1151
Scotland N667, K107
Senegal N888 (W. Rothschild)
South Africa, Republic of N649, N1167, N1167a, K50, K142
Sri Lanka K35, K54
Switzerland N619, N624, N625, N1069, N1161

Tanzania K52, K62, K68, K69, K70, K71, K72, K73, K74, K83, K97, K131, K143
Tibet K86
Trinidad-Tobago K53

Uganda-Zaire border N559
Unknown N549, N554, N555, N558a, N558b, N564, N565, N570, N574, N575, N575x, N584, N585, N589, N590, N591, N613, N617, N634, N637, N638, N639, N826, N1066, N1153, N1154, N1164, N1395, N1398, N3138, N3330, (N75), (N77), (N78), (N90), (N91), (N92), (N516), (N517), (N548), (N586), (N587), (N595), (N620), (N628), (N629), (N632), (N674), (N3136), (N3139), (N3140), (N3141), (N3157), (N3351), K14
U.S.A. N594, N626, N666, N1399, K4, K7
U.S.S.R. K56

Venezuela K113

Wales N606, N609, (N746), K109

Yugoslavia K106

Zambia K135

Zimbabwe N577, N578

Host list for ticks in the Rothschild collection

Numbers in parentheses indicate missing collections. All information relating to missing collections is taken directly from Nuttall's catalogue or British Museum (Nat. Hist.) collection cards.

Alces alces N1497, N1499
Anaconda (N3141)
Anomalurus derbianus jacksoni K98
Anteater K24
Armadillo K34
Arvicola terrestris N662
Ateles geoffroyi geoffroyi N565, N640

Bat N591, K120, K123
Bettongia lesueri N646
Bettongia penicillata N1393
Bird (N397)
Blastoceros bezoarcticus K21
Boa (N548)
Bradypus tridactylus (N544), (N3351)

Camel (N586)
Canis familiaris N572, N573, N576, N579, N645, N892, K9, K38, K56, K60, K83, K86, K110, K116, K135, K136, K137
Canis, sp. K19
Canis vulpes (N217)
Cat (K151)
Cat, black N504
Cat, wild K82
Cattle K9
Cercartetus concinnus N1162
Cervus capreolus (N509)
Chicken K4
Clethrionomys glareolus N619, K118
Coendou bicolor simonsi N560
Coendou prehensilis K18
Columba livia K3
Cricetomys gambianus K115

Dactylopsida trivirgata K100
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Synopsis

Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic are revised. Of more than three hundred nominal species just twenty-three are regarded valid. Their taxonomy, nomenclature, morphology, ecology, reproduction, distribution and relationships are discussed and a key is provided for their identification. The genera occurring in the eastern North Atlantic are revised in detail. In addition the genera not represented in this area are briefly reviewed and notes are included to update a previous revision of the genus *Obelia*.

Type designations

Type material is designated of the nominal species *Campanularia laevis* Couch, 1844, to facilitate comparison with *Campanularia laevis* Hartlaub, 1905, for which a new name is proposed (p. 54). Lectotype material is designated of *Sertularia uniflora* Pallas, 1766 (p. 78), *Laomedea gracilis* Sars, 1850 (for which a new name is proposed, p. 78), and *Campanularia intertexta* Couch, 1844 (p. 122).

Type species are designated of two genera and a subgenus: *Cymodocea* Lamouroux, 1816, family Plumulariidae (p. 121); *Eucope* Gegenbaur, 1856 (p. 71); subgenus *Eucampanularia* Broch, 1910 (p. 52). The type genus of the subfamily Clytiinae nom. nov. is designated as *Clytia* Lamouroux, 1812 (p. 69), and that of the subfamily Phialiinae (Family Lovenellidae) as *Phialium* Haeckel, 1879 (p. 69).

Introduction

The family Campanulariidae is represented in all oceans. The species are found mainly within continental shelf depths, and some occur intertidally. Many of the genera and species are cosmopolitan. For example, many of the species recorded from New Zealand by Ralph (1957) occur also in British waters (see Geographical distribution, p. 44).

Several European authors have revised the species of Campanulariidae recorded from their home waters (e.g. Hincks, 1868; Linko, 1911; Broch, 1918; Nobre, 1931; Kramp, 1935; da Cunha, 1944; Vervoort, 1946*a*; Leloup, 1947; Russell, 1953; Naumov, 1960, 1969; Patriti, 1970; Rossi, 1971). But apart from the synoptic lists of Bedot (1901, 1905, 1910, 1912, 1916, 1918, 1925) and a review of the genus *Obelia* (by Cornelius, 1975*a*) there has been no previous attempt to compare the nominal species recorded from the whole of the eastern North Atlantic. As a result many straightforward taxonomic questions have been left unresolved. No doubt the wide range of phenotypic variation typical of this family has caused problems. But it is apparent also that the wide geographical ranges of many of the species has led to unwitting duplication of work between countries. The resulting literature is widely scattered, and this too has imposed problems since only a few libraries have all the relevant publications.

This report attempts to revise the species of the family Campanulariidae, excepting those in the genus *Obelia*, recorded from the eastern North Atlantic. *Obelia* is excluded since it was revised recently (Cornelius, 1975*a*) but notes are included to update that revision. The area extends southwards to the equator and west to the 30° meridian. It includes the Mediterranean, Black and Baltic Seas, and extends in one region beyond 30° W to include the coastal waters of Greenland. In general there have been few records of the family north of 80° N, but this must reflect collecting difficulties since several species have been reported from these high latitudes (Linko, 1911). One dubious tropical species, *Orthopyxis africana,* is not treated fully because it has been recorded only once, near the southern limit of the area.

Most genera of Campanulariidae are nearly cosmopolitan. It happens that the majority are represented in the eastern North Atlantic. Further, most were described first from European waters; so that a revision of the NE Atlantic genera comes close to a complete revision. A comprehensive generic synopsis is not intended here, however, since not all the nominal species are covered. But at least an interim generic list can be given (Table 1). Most of the nominal genera are discussed, whether or not they have been recorded in the NE Atlantic, and the relevant discussion sections can be found through the index. All are at least mentioned.

Table 1 The subfamilies and accepted genera of the Campanulariidae. Those not recorded from the NE Atlantic are treated only briefly in this paper, and are marked by an asterisk.

Subfamily/genus	Recent redefinition, if any	Notes
CAMPANULARIINAE	p. 50	
Campanularia Lamarck, 1816	p. 51	
**Eucalix* Stechow 1921*a*		p. 50
**Orthonia* Stechow, 1923*a*		p. 51
Orthopyxis Agassiz, 1862	p. 58	
Rhizocaulus Stechow, 1919*b*	p. 67	
**Silicularia* Meyen, 1834	Ralph, 1957; Stepanyants, 1979	p. 50
CLYTIINAE *nom. nov.*	p. 69	
Clytia Lamouroux, 1812	p. 71	
**Gastroblasta* Keller, 1883	Kramp, 1961	p. 72
**Tulpa* Stechow, 1921*a*	Ralph, 1957; Stepanyants, 1979	p. 70
OBELIINAE Haeckel, 1879	p. 91	
Gonothyraea Allman, 1864*a*	p. 92	
Hartlaubella Poche, 1914	p. 94	
Laomedea Lamouroux, 1812	p. 97	
Obelia Péron & Lesueur, 1810*a*	p. 112	

Taxonomy and the phenotype

The long synonymies and remarks sections in this paper and in that on *Obelia* (see Cornelius, 1975*a*) reflect the fact that wide phenotypic variation has led to nominal taxa being based on unimportant characters. Even the usually reliable Hincks (1868) was misled; but in fairness it should be remembered that Hincks, and his colleagues Alder and Allman, were breaking new ground when seriously considering the taxonomy of this family. Now, with a century of hindsight, the taxa they and others proposed can be better assessed. The early workers did not realize how much these hydroids vary, compared with the usually much less variable species of Haleciidae, Sertulariidae and Plumulariidae which they knew already.

Some of the literature on variation in the species of this and other thecate families has been reviewed recently (Cornelius, 1975*a*, *b*, 1979). The notes in the 1975*a* paper, on *Obelia*, are now summarized and this is followed by some new comments. Authorities for the species names are mostly omitted here since they are adequately indicated in the Taxonomic Section (p. 47).

Colony size in erect species probably increases till mechanical breakage occurs (Crowell & Wyttenbach, 1957, in *Laomedea flexuosa*; Cornelius, 1975*a*, in *Obelia dichotoma*) and is of little taxonomic value. *Obelia geniculata* growth was studied by Ralph (1956) and Ralph & Thomson (1968) in New Zealand. Growth was faster in cool conditions than warm.

Polysiphonic stems occur sometimes in *Obelia dichotoma* (*cf.* Millard, 1973) and *Laomedea neglecta*, and are usual in *Hartlaubella gelatinosa* and *Rhizocaulus verticillatus*. The species *Obelia plicata* Hincks, 1868, was based on *O. dichotoma* material of this kind (p. 119). Occasional overgrowth of one colony by another of the same species is a rather different phenomenon now called auto-epizoism (p. 119).

Branching was most frequent in low water temperatures in *Obelia geniculata* in New Zealand (Ralph & Thompson, 1968). Similar results were obtained from '*Clytia attenuata*' by West & Renshaw (1970) who discussed the taxonomic implications (see also notes on Growth, p. 42).

Internode length, extent of annulation, curvature, amount of asymmetric thickening and angle of flexure have all be used to define species limits in the Campanulariidae; but only asymmetric thickening (in *Obelia geniculata*) and sometimes curvature (in *Laomedea flexuosa*) seem good characters (Cornelius, 1975*a*; below, p. 113).

Perisarc tanning has been included in some species descriptions, for example in that of the now discredited *Obelia longissima* (discussion in Cornelius, 1975*a*), but has not been taken as a unique species character. The intensity of tanning increases with age in many species. In some the perisarc does not seem to darken appreciably, but this might be due simply to its thinness. Knight (1965, 1970, 1971) studied the tanning process in *Laomedea flexuosa.*

Hydranth characters are not useful at species level but the shape of the hypostome is consistent throughout some genera. Tentacle number is usually too variable to be useful, notably in *Clytia hemisphaerica* and *Obelia dichotoma*, but it has been used in defining *Orthopyxis crenata.*

Hydrothecal characters are useful in this family. But despite their confusing intraspecific variation (Broch, 1910, and later workers) we hardly know how the characters develop (e.g. Berrill, 1949, in *Obelia*; Berrill, 1950, in *Clytia hemisphaerica, Laomedea flexuosa* & *Orthopyxis integra*; Knight, 1965, in *Laomedea flexuosa*; Beloussov, 1973, in *Gonothyraea loveni*). Several authors have reported chitinous structures in the hydrothecae of *Gonothyraea loveni* and *Obelia bidentata* which, however, have proved merely to be regularly arranged folds in the delicate hydrothecal walls. Minor variations in the pattern of cusps on the hydrothecal rims of several of the species have been given undue weight by some authors (see Remarks under *O. bidentata*). Presence or absence of the hydrothecal diaphragm is a subfamily character but is not useful at genus or species level.

Mammen (1965) noted that an oblique hydrothecal diaphragm viewed from the 'front' appears transverse in optical section—a point not realized by some taxonomists. It follows that rotation of a sloping diaphragm produces a whole series of angles, from horizontal to the true maximum slope. Further, even when correctly viewed, a transverse diaphragm is not a consistent character (Cornelius, 1975*a*).

Naumov (1969 : 123) stated that many hydroids have larger hydrothecae in cool waters than warm, but offered data in only one species (*Orthopyxis integra*). Although the relation might well be valid in many species, detailed proof is needed. Possibly it has already caused taxonomic confusion since large, northern specimens of *Clytia hemisphaerica* have been referred to the invalid *C. gigantea* by several authors (p. 81)—but not all of the large specimens were from cool areas.

Hydrothecal pedicels are variable in length, in amount of annulation and in the presence or absence of a smooth central portion. Most species vary widely in these characters. Pedicels of reptant species are usually longer than those of upright colonies, perhaps in response to greater feeding opportunities away from the substrate than close to it. A peculiar case is the long hydrothecal pedicels of floating colonies of the usually reptant *Clytia hemisphaerica,* which have often been regarded a distinct species (*C. sarsi* nom. nov., p. 78). Implicitly, minor variations in pedicel length are phenotypic and overall length ranges are genotypic; but evidence is lacking.

A more useful pedicel character than length is the occurrence of spiral grooving in some species in place of the more usual annuli. Spiral grooving seems constant in those species having it, and has not been found even exceptionally in annulated species; but annulated pedicels have been recorded in the usually smooth to spiral *Rhizocaulus verticillatus* (p. 68). When present a spirally ornamented pedicel is a safe character.

Another reliable character is the formation in some species of a sub-hydrothecal 'spherule', first described by Ellis (1755) and noted by many subsequent authors. It is formed between two annuli just below the hydrotheca and spaced apart on the pedicel by a distance about equal to its width (Fig. 6). Some authors have regarded possession of spherules by distinct species as indicating affinity, and this seems usually justified. But spherules are simple modifications of existing structures and might have evolved more than once. Thus *Clytia hummelincki* is alone in its genus in having a spherule.

The spherule structure is otherwise found in the genera *Campanularia, Orthopyxis* and *Rhizocaulus*. It recalls the basic arthropod joint in having structures analogous to arthrodial membranes, but in other ways it resembles the vertebrate ball-and-socket joint. Considerable passive flexibility is achieved with little materials, enabling the hydrotheca to be rapidly orientated downstream in response to local water movement. It would seem that fewer materials are needed in this arrangement than would be needed to construct a rigid, unbending pedicel which could maintain the hydrotheca broadside on in strong currents. The spherule joints seem to be an evolutionary advance on the simple annulations seen in many species of Campanulariidae. Uniformly annulated pedicels bend a little at each annulation and have tissue-attachment problems associated with repeated asymmetric compression along their whole length. A hydrotheca supported by a spherule can simply flip-flop from side to side in response to local current surges, and bends just at one point. In addition, spherules would appear more resistant to vertical compression than annuli.

Murdock (1976) considered very briefly the role of annuli in *Obelia* sp. main stems. He observed that they help bending, an obvious conclusion not often repeated. Hughes (1980) studied *Laomedea flexuosa* and *Obelia dichotoma* at a few sites on British coasts and found higher numbers of pedicel annuli in sheltered situations than exposed.

Gonothecal shape provides good taxonomic characters in *Laomedea* but in *Clytia, Obelia* and *Orthopyxis* it does not. Some nominal species have been based on immature gonothecae, for example the invalid '*Laomedea conferta*' (p. 104).

Most species have monomorphic gonothecae but strongly marked sexual dimorphism does occur. It has caused taxonomic confusion in *Laomedea calceolifera*, which was formerly regarded as two species. The two kinds of gonothecae proved to be male and female of the same species. Gonothecae of *L. angulata, L. flexuosa* and *Gonothyraea loveni* tend towards sexual dimorphism, and the few *L. pseudodichotoma* specimens available indicate it occurs in that species too. In the other species described herein the gonothecae are monomorphic, so far as is known.

Nematocysts have not yet proved useful in delimiting species in *Obelia* (Cornelius, 1975*a*) but little is known of their potential value in the rest of the family (review in Östman, 1979). As in most hydroids, they are among the smallest of nematocysts and their study requires refined techniques. Although Östman reported slight differences in basal armature between the nematocyst threads of some pairs of species here regarded conspecific [*Clytia hemisphaerica* (Linnaeus, 1767) and *C. sarsi* nom. nov. (=*Laomedea gracilis* Sars, 1850); *Obelia dichotoma* (Linnaeus, 1758) and '*O. longissima* (Pallas, 1766)'], rather few populations have yet been studied. She commented that microbasic mastigophores have hitherto been separated on characters which are optical artefacts, a conclusion borne out by some unpublished electron micrographs she has kindly shown me (Östman, pers. comm.). If the populations having distinct, although very similar, nematocyst types can be distinguished on other characters also then Östman's conclusions will be corroborated. But the undischarged capsules are only 6 μm to 8 μm long, and the fine details of thread structures are unlikely to prove useful in routine identification. Some correlation with gross morphological characters would seem desirable. See also page 78 concerning '*Clytia gracilis* (Sars, 1850)'.

Habitat preferences and substrate associations are discussed under ecology. Few members of the family have a regular habitat association and most seem able to live on a wide variety of substrates. The prime exception is *Laomedea angulata*, living exclusively on eel grasses; but since other hydroids live there too this does not help in identification.

Medusa generation Russell (1953) showed best the extent to which intraspecific variation in hydromedusae has led to many invalid species being described; but the factors controlling this apparently phenotypic variation are almost unknown.

The problems surrounding the two nominal species of *Obelia* recognized from the medusa stage in British waters still remain (summarized in Cornelius, 1975*a*, but based largely on Russell, 1953 and pers. comm.). In addition there is no clue as to why *Obelia* medusae on release should not always be at the same stage of development. Some authors have based nominal species of *Obelia* partly on tentacle number at the time of release, and although this seems unwise the cause of the variation is still unexplained.

In contrast, four tentacles on release is characteristic of the medusae of most of the *Clytia* species (see generic diagnosis, p. 71). Adult medusae of *Clytia linearis, C. hummelincki, C. paulensis* and *Orthopyxis crenata* (but see p. 59) are undescribed, as are the hydroid stages of *C. discoida*, *C. pentata*, *C. islandica* and arguably *C. mccradyi.* When all stages in the life cycles of these species are known some of the nominal taxa may fall.

It is remarkable that only a little taxonomic confusion has resulted from the unusual habit in *Orthopyxis integra* of releasing medusae on some occasions and not on others (p. 63).

Growth is affected by many factors and has been widely studied in this family. Hammett (1943) is now thought to have studied growth in *Laomedea flexuosa,* not *Obelia geniculata* as he stated (Crowell, 1957; Cornelius, 1975*a*). Toth (1969) studied colony 'senescence' in *L. flexuosa.* Wyttenbach, Crowell & Suddith (1973) reviewed their own work on stolon elongation in thecate and athecate hydroids, treating *Laomedea calceolifera, L. flexuosa* and *Gonothyraea loveni* among the present family. They reported similar results in the two *Laomedea* species but found generic differences in the growth cycles of the stolon tips. Cyclic increases in length had been demonstrated earlier in *L. flexuosa* by Wyttenbach (1968, 1969) alone; and Beloussov (1961) and Hale (1964) had still earlier found the same peculiar phenomenon in stolons of *Laomedea flexuosa* and *Clytia hemisphaerica* respectively. Hale (1973*a, b*) later reported further morphogenetic work on *C. hemisphaerica* stolons and reviewed the literature. Beloussov's (1973) important paper described more work on the stolons of *G. loveni* but he did not take environmental factors into account. Nevertheless, phenotypic responses to changes in temperature and feeding opportunity are known to occur in the stolon of *L. flexuosa* (e.g. Crowell, 1957, 1961), mainly in 'alterations largely due to the sensitivity of zones of prospective growth'. These observations are interesting in themselves, but their experimental requirements make them unsuitable for regular taxonomic use.

Phenotypic response to temperatue change was noted in the hydroid stage of '*Clytia attenuata*' by West & Renshaw (1970) who incidentally regarded that species as valid (but see p. 40). In vitro colonies at 13°–15°C were unbranched and could not be distinguished from '*Clytia cylindrica* Agassiz'; but at 17°–19°C a kind of branching occurred which these authors considered characteristic of *C. attenuata.* Whatever the validity of the two nominal species involved, West & Renshaw drew attention to a taxonomic difficulty resulting from phenotypic response. Their extensive review and discussion mainly concerns western North Atlantic species of *Clytia* hydroids and medusae, and further comment would be out of place here.

Finally Stebbing (1976, 1979, 1981; see also p. 107) has studied the influence of toxic inorganic ions on the growth and death of *Laomedea flexuosa*. He found that growth was actually enhanced at sub-inhibitory concentrations of the toxic ions. It seems that care should be taken when assessing the morphological characters of material collected from slightly polluted places.

Ecology

Associations. Only one of the species included here has an apparently obligatory substrate association: *Laomedea angulata,* which has been reliably recorded growing only on eel grasses. *Obelia geniculata* tends to occur on brown algae whereas the very similar *O. dichotoma* grows usually on other substrates; but each occurs occasionally on the substrate more usual for the other. The other North Atlantic species of the family show no marked substrate associations. They repeat the general hydroid pattern of a few species having some substrate specificity with the majority having only loose associations or none at all; but the association of *L. angulata* with eel grasses is unusually close. Nishihira (1968) reported '*Clytia edwardsia*' to be 'characteristic of' *Zostera marina* in Japanese waters. However, both Nishihira and Picard (1955, in Algeria) reported many hydroid species growing on *Zostera* but not confined to it.

Brackish water and estuarine species. Many species of Campanulariidae are tolerant of reduced salinity. But while many of the species included here occur either occasionally or habitually in low salinity areas, none has been reported from fresh water. The species comprise more than a third of the present faunal list: *Laomedea angulata, L. calceolifera, L. neglecta, Clytia paulensis, Gonothyraea loveni, Hartlaubella gelatinosa, Obelia bidentata, O. dichotoma* and *O. geniculata.* All records refer to the hydroid stage and none to the medusa. Further details are given in the Habitat sections of these species.

A similar impression of the family was given by Calder (1976). He found as many as 40 brackish water hydroids in South Carolina, and of these no fewer than ten were from the Campanulariidae.

Interactions between species. Although the phenomenon of overgrowth has been studied in a variety of coelenterates and other colonial invertebrates (review in Larwood & Rosen, 1979), among hydroids it has been recorded infrequently. Sustained overgrowth of one hydroid colony by another is unusual, and in the present family there are a few instances only. For example, occasional colonies of *Obelia dichotoma* with erect stems comprising more than one hydrocaulus were once regarded a distinct species (*O. plicata*, p. 119); and the regularly polysiphonic stems of some other species treated here may be derived in the same way (*Rhizocaulus verticillatus,* p. 67; *Hartlaubella gelatinosa*, p. 95; *Obelia bidentata*, p. 113). Overgrowth has been recorded occasionally in *Laomedea neglecta* (p. 107) but the species is not well enough known for this to be assessed. Millard (1973) listed several species of thecates from other families showing growth of one colony on another, and introduced the descriptive term auto-epizoism.

Antagonism between colonies is widely known among other coelenterates and in many of the invertebrate phyla (Larwood & Rosen), but like overgrowth has seldom been reported among hydroids. Hughes (1975) reviewed work on a few species of Campanulariidae ('*Clytia volubis* Packard', *C. hemisphaerica, Obelia dichotoma*); while in another family Warburton (1953) recorded aggression between a colony of *Hydractinia echinata* (Fleming, 1828) and one of *Podocoryne ?carnea* Sars, 1846, on a gastropod shell inhabited by *Pagurus* sp.

Geographical distribution

Most species of Campanulariidae are widely distributed, some occurring nearly throughout the World in shallow waters. For example, of the 18 species recorded from New Zealand no fewer than seven occur also in British waters (Ralph, 1957). The corresponding figures for southern African seas are 21 species and 8 (after Millard, 1975; the immigrant *Gonothyraea loveni* would be additional), and for the antarctic area 13 and five (after Stepanyants, 1979, with some taxonomic revision). But few species of the family appear uniformly distributed, and many have a patchy local distribution. The local variations are best documented in European waters, towards which the following notes on the eastern North Atlantic species are unavoidably biased. Further details are given in the Taxonomic Section under each species.

Orthopyxis integra. Although one of the most nearly cosmopolitan of all shallow-water hydroids this species has not been found in the Kattegat, Skagerrak, Baltic Sea and Dutch waters; and has only occasionally been recorded from Belgium, western Scotland and the Irish Sea.

Clytia hummelincki. So far this species has been reported only from the West Indies, Florida, Massachusetts, South Africa and Ghana (p. 83).

Clytia paulensis. Known for some years from parts of NW France but only recently added to the British faunal list (p. 89). However, a specimen collected in S Devon in 1899 has now been correctly identified. In the 1970s the species was found in Devon and Suffolk.

Gonothyraea loveni. In South Africa this species is known from Cape Town docks only, and Millard (1975) considered it had spread from Europe to the Southern Hemisphere on ships.

Hartlaubella gelatinosa. The several nineteenth century Scottish records contrast with a single Scottish record this century, in 1932 (p. 95). But the species is still common at least as far north as NW England (J. Clare, pers. comm.) and the lack of recent Scottish records may be misleading.

Laomedea angulata. There are few reliable records from the British Isles this century, in contrast to an abundance of nineteenth century records (p. 100). Apparently the species has yet to regain its former distribution after the temporary decline of the *Zostera* beds in the 1930s (described by Tutin, 1942). Although *L. angulata* was recorded from the Scillies in 1967 (Robins, 1969) there is apparently no other reliable British record since those from S Devon before 1910 (Marine Biological Association, 1957). (But see Addendum.)

Laomedea calceolifera. Although widespread in North Atlantic waters, relatively conspicuous, and distinctive when fertile, this species has been reliably recorded only twice from British waters (S Devon, *c.* 1871, by Hincks, 1871; Norfolk, in 1951, by Hamond, 1957), with a third dubious record (Norfolk, in 1899, quoted by Hamond, 1957). Probably the species reaches its northern limit in southern England but the paucity of British records is still remarkable as the species is well known from NW France (p. 104).

Laomedea pseudodichotoma. This species has yet to be recorded away from the coastal waters of tropical W Africa but it would be remarkable if this indicated the true geographical range (p. 112).

Obelia bidentata. This species was first reported from British waters only some 25 years ago; and the first record from the south coast of England is reported here (p. 115). It seems unlikely that the nineteenth century British collectors would have overlooked so distinctive a species, and the absence of earlier records may be genuine. The species was not known in Europe until the 1900s. Indeed, it may have been an immigrant into E Atlantic waters from the American coast, but this is not certain and early confusion with *Hartlaubella gelatinosa* is not excluded as a reason for the absence of earlier records. See also the next species.

Obelia dichotoma & *O. geniculata*. There are records of these widespread species on many swimming vertebrates, including a turtle, a shark, the blueback herring and a sea-horse; and also on drifting kelp (pp. 117, 118, 120). Taken together the records suggest that these species might be transported over vast distances. The potential was realized long ago in other hydroid families (e.g. Alcock, 1892; Lloyd, 1907; Heath, 1910; review in Gudger, 1928, 1937). Transport might explain the appearance of the previous species in European waters around the 1900s, carried perhaps by ships rather than by vertebrates. However, turtles regularly cross the Atlantic (Parker, 1939; E. N. Arnold, pers. comm.) so that natural means are not excluded. *Clytia hemisphaerica*, another widespread species, has similarly been found on fish, attached to their crustacean ectoparasites (p. 77). It seems plausible that continuous transport across deep ocean basins will promote exchanges between the gene pools of these species on different continental shelves; and might explain why many hydroid species are virtually cosmopolitan at shelf depths. Paradoxically, it may be that the hydroid stages of such species sometimes travel further than their medusae which live for just a few weeks.

Key to species (hydroid stages)

Many of the species of Campanulariidae are so variable that overlap in characters occurs, and identification by a dichotomous key is not always possible. Young and infertile specimens are particularly difficult and even with the help of long Museum series some specimens cannot be identified. Close study of a single, undamaged hydrotheca is often useful and the outline of the unabraded rim can be diagnostic. Hydranth characters are seldom useful for identification in this family.

Provisional identification can frequently be made from the illustrations of the gonothecae. Characters based on reproductive structures are mostly omitted from the key, however, as many specimens are infertile. When identifying fertile material it can be helpful to determine whether the ova develop within the gonotheca or in an external acroyst, and if the gonotheca contains developing medusae; but these characters too are mostly avoided in the key.

1	Colony with erect stems each supporting several to many hydrothecae	2
–	Colony mainly stolonal, each stem or pedicel supporting one or just a few hydrothecae	18
2	Rim of hydrotheca even to sinuous	3
–	Rim of hydrotheca definitely cusped [Rims often abrade smooth in *Gonothyraea loveni, Hartlaubella gelatinosa* and *Laomedea neglecta*]	10
3	Terminal region of hydrotheca flared	4
–	Terminal region of hydrotheca not flared	5
4	Gonothecal aperture narrow; recurved in mature ♀	*Laomedea calceolifera* (p. 102; Fig. 18)
–	Gonothecal aperture broad, never recurved [tropical]	*Laomedea pseudodichotoma* (p. 111; Fig. 21)
5	Internodes curved	6
–	Internodes straight	8
6	Hydrotheca thickened, sometimes much so	*Obelia geniculata* (p. 119)
–	Hydrotheca with little or no thickening	7
7	Hydrotheca usually 1½ times long as broad, or longer; gonothecal aperature usually raised; releases medusa	*Obelia dichotoma* (p. 117)
–	Hydrotheca not much longer than broad; gonothecal aperture not raised; no medusa stage	*Laomedea flexuosa* (p. 105; Fig. 19)
8	With sub-hydrothecal spherule [a locally distributed species]	*Clytia hummelincki* (p. 82; Fig. 10)
–	Lacking sub-hydrothecal spherule	9
9	Internodes rigidly straight; terminal tendrils present in autumn; gonotheca borne on stolon; no medusa [on eel grass]	*Laomedea angulata* (p. 98; Fig. 17)

– Internodes slightly curved; terminal tendrils unusual; gonotheca nearly always axillary; medusa released [on many substrates, but including eel grass] . *Obelia dichotoma* (p. 117)

10 Hydrothecal cusps sharp 11
– Hydrothecal cusps blunt, square, notched or rounded 15

11 Hydrothecal cusps usually bimucronate (hard to see; four species difficult to separate when immature) 12
– Hydrothecal cusps all same length *Clytia hemisphaerica* (p. 73; Fig. 9; see also *C. mccradyi* p. 87, Fig. 13)

12 Mature colony tall and bushy, with polysiphonic stem and second-order branching; gonothecal aperture usually raised, slightly narrower than gonotheca *Obelia bidentata* (p. 113)
– Mature colony small, with up to *c.* 20 hydranths; stem monosiphonic (except occasionally in *L. neglecta*); gonothecal aperture not raised, as broad as gonotheca 13

13 Hydrothecal pedicels longer than hydrotheca . . . . *Clytia paulensis* (p. 88; Fig. 14)
– Hydrothecal pedicels roughly same length as hydrotheca or shorter 14

14 Each internode of constant diameter; hydrothecal cusps strengthened by substantial chitinous strip; medusa released [Mediterranean southwards] . . *Clytia linearis* (p. 84; Fig. 12)
– Internodes slightly bulging; hydrothecal cusps without strengthening strip (folds in hydrothecal wall can be confusing); no medusa [Mediterranean northwards] (see also young *Obelia bidentata*) . . . . *Laomedea neglecta* (p. 107; Fig. 20)

15 Hydrothecal margin with rounded cusps 16
– Hydrothecal margin with square cusps, often notched (abrade easily). 17

16 Mature colony large, polysiphonic; most hydrothecae with subhydrothecal spherule; no medusa stage . . . . *Rhizocaulus verticillatus* (p. 67; Fig. 7)
– Mature colony not usually large, always monosiphonic; no spherule; medusa released *Clytia hemisphaerica* (p. 73; Fig. 9) (also *C. mccradyi*, ?S France only; p. 87; Fig. 13)

17 Small slender colony, stem monosiphonic; primary branching only; medusa retained as gonomedusa external to gonotheca . . . . *Gonothyraea loveni* (p. 92; Fig. 15)
– Large bushy colony, stem polysiphonic; with secondary branching; large ova, developing into planulae within gonotheca; no medusa. . *Hartlaubella gelatinosa* (p. 95; Fig. 16)

18 Sub-hydrothecal spherule present 19
– Sub-hydrothecal spherule absent 24

19 Rim of hydrotheca even 20
– Rim of hydrotheca cusped or undulating 21

20 Hydrotheca usually much thickenend [common] *Orthopyxis integra* (p. 60; Fig. 6) (also *O. crenata* with even hydrothecal rims; see text)
– Hydrotheca unthickened [scarce] . . . . *Clytia hummelincki* (p. 82; Fig. 10)

21 Hydrotheca > 0·5 mm long, with lines running downwards from rim (sometimes absent in one species) 22
– Hydrotheca < 0·5 mm long, without lines 23

22 Lines meeting tips of cusps, which are roundly pointed, not notched; hydrotheca 2+ times long as broad [probably not south of Newfoundland and Spitzbergen] *Campanularia crenata* (p. 52; Fig. 2)
– Lines meeting bottoms of embayments; cusps flat-topped with notch; hydrotheca up to 1·5 × long as broad [widespread] . . . . . . *Campanularia hincksii* (p. 53; Fig. 3)

23 Hydrotheca usually much thickened [probably Mediterranean southwards] *Orthopyxis crenata* (p. 58; Fig. 5)
– Hydrotheca unthickened [Mediterranean northwards] . *Campanularia volubilis* (p. 55; Fig. 4)

24 Hydrothecal cusps bimucronate [S England southwards] . *Clytia paulensis* (p. 88; Fig. 14)
– Hydrothecal cusps simple [widespread] *Clytia hemisphaerica* (p. 73; Fig. 9; also *C. mccradyi*, ?S France only; p. 87; Fig. 13)

Taxonomic section

Family CAMPANULARIIDAE Johnston, 1836

DIAGNOSIS. Colonial Thecata (sens. Millard, 1975); hydroid stage stoloniferous or erect, stolon when present may be branched or unbranched; hydrotheca bell-shaped, radially symmetrical, pedicellate, with diaphragm and an associated annular thickening, or with annulus alone and without diaphragm; no operculum; hydranths radially symmetrical, usually with prominent hypostome; no caecum; one ring of tentacles; nematophores absent; ♂ & ♀ gonothecae usually externally identical. Medusa generation when present variable; reduced in *Obelia* and (?) facultatively retained in *Orthopyxis*; typical leptomedusan in *Clytia* and *Gastroblasta*; always retained as gonomedusa in *Gonothyraea*; identifiable in more reduced form in at least some other genera and species.

REMARKS. The family was first proposed by Johnston (1836, 1847, but not 1838). Originally *Lafoea dumosa* (Fleming, 1820) was included in its scope but was removed to the Lafoeidae by Hincks (1868). The limits of the family have remained unchanged ever since and the redefinition by Millard (1975) seems sound. Ralph (1957) also provided a detailed appraisal.

Much has been written about generic limits within the family but it is convenient to go no further back in the literature than the works of Broch (1905, 1910) and Goette (1907). Broch recognized two broad genera. These he called *Campanularia* Lamarck, 1816, which had no hydrothecal diaphragm, and *Laomedea* Lamouroux, 1812, which had one. He divided his concept of *Campanularia* into the subgenera *Eucampanularia* Broch, 1910, having sessile gonophores, and *Clytia* Lamouroux, 1812, with free medusae. Broch split his other broad genus concept, *Laomedea*, into the three subgenera *Eulaomedea* Broch, 1910, with sessile gonophores and no medusoid structures; *Gonothyraea* Allman, 1864*a*, with retained 'eumedusoids' (now called gonomedusoids, p. 93); and *Obelia* Péron & Lesueur, 1810*a*, with free medusae. Thus Broch's basic division within the family was on a hydrothecal character; while within each of the two main divisions his classification was on the state of reduction of the medusa generation (following and elaborating on the interpretation of these structures by Goette, 1907).

Splettstösser (1924 : 424–425) followed Broch's system but further split Broch's subgenus *Eulaomedea* into one group with intracapsular gonophores ('*Laomedea gelatinosa*', *L. flexuosa* and *L. calceolifera*) and a second, in which the mature gonophores were extracapsular (*L. neglecta*). Splettstösser acknowledged that the classification might be criticized since just a small number of species was considered. But Broch (1928) gave it support when he later introduced the subgeneric name *Paralaomedea* for the '*L. neglecta* group', comprising that species alone, in the combination '*Laomedea* (*Paralaomedea*) *brochi* Splettstösser (= *Laomedea neglecta* Alder)'. [Splettstösser's restriction of the subgenus concept was thus cited as indication by Broch; but the authority for the associated subgenus name *Paralaomedea* was Broch (1928).] Finally Hummelinck (1936) redefined the subgenus rather tightly, again to include only *L. neglecta*.

As Splettstösser had commented, very few species were considered in his classification and it is questionable whether so many infra-generic divisions were justified. (Some additional sub-divisions of '*Eulaomedea*' proposed by Splettstösser were not given names, and are not mentioned here.) His own work on *L. neglecta* and other species, and that for example of Goette (1907) and Miller (1973), emphasized that the gonophore 'types' identified by Splettstösser form part of a series in which the medusa is progressively reduced. The gonophore of *L. neglecta* seems simply to fit into this series. Further, Broch's (1910) primary division of the family into two was on the basis of a single hydrothecal character, and this division too might be challenged.

The extent to which the medusa-medusoid-gonomedusoid-gonophore series should be classified into genera will perhaps be debated for as long as the series is regarded valid. But today as in Broch's time, most is known about the life-cycles of the western European species. Until more information is available on species from other parts of the World it seems unwise to split *Laomedea* into subgenera.

Aside from the taxonomic debate, there are some nomenclatural problems which need solution. These I have considered in a submission to the International Commission on Zoological Nomenclature (Cornelius, 1981). The aims of the proposals are provisionally included in the present paper.

The subgenera proposed by Broch, Splettstösser and others need not be recognized. But the evolutionary fate of the medusa generation is still reflected in the classification adopted here. In *Orthopyxis* the medusa is reduced and lacks several normal adult characters, functioning simply as an ephemeral gamete carrier. It is thought to be facultatively released in some or all of the *Orthopyxis* species (see p. 63); while in the closely related *Orthonia* it is still further reduced, to a retained acrocyst. In *Campanularia, Rhizocaulus* and *Silicularia* the gonosome has become intracapsular, with no obvious indications of a medusoid ancestry.

A parallel series showing progressive retention of the medusa can be demonstrated within the genera *Obelia, Gonothyraea, Laomedea* and *Hartlaubella*. In *Obelia* the medusa is released. The extra-capsular gonomedusoids of *Gonothyraea* are easily identified as retained and vestigial medusae; and in *Laomedea* it has been shown that the gonosomes of several species represent reduced medusae. Indeed, so reduced has the medusa generation of *Laomedea* become that until the work of Miller (1973; see also Goette, 1907) the medusoid nature of the gonophore was not appreciated. The same confusion prevailed also in interpretations of the reproductive structures in *Orthopyxis integra*, in which the medusa is sometimes retained. It was thought until quite recently that the retained examples had 'sporosacs' in place of medusae, and that they might therefore be a different species (*O. caliculata*; p. 65–66)!

The genera *Clytia, Gastroblasta* and *Tulpa,* which have a true hydrothecal diaphragm and sub-hydrothecal spherules, apparently form another group but their relation to the rest of the family is not clear.

The three series recognized are shown in Figure 1. The groupings seem natural and are here given subfamily status: Campanulariinae (p. 50), Clytiinae nom. nov. (p. 69) and Obeliinae Haeckel, 1879 (p. 91). See also page 49.

The generic limits suggested by Millard (1975) are slightly modified, as is her nomenclature. *Orthopyxis* is here separated from *Campanularia* sens. Millard. *Eulaomedea* sens. Millard is here called *Laomedea. Sertularia gelatinosa* Pallas, 1766, not in Millard's faunal area, is referred to the monotypic genus *Hartlaubella*; and another species not in her list, *S. verticillata* Linnaeus, 1758, is here referred to the nearly monotypic *Rhizocaulus.*

To promote stability of nomenclature I have attempted to include all extra-limital generic synonyms. The valid genera found outside the NE Atlantic are treated briefly. They are *Eucalix, Orthonia* and *Silicularia* from the Campanulariinae (p. 50); and *Gastroblasta* and *Tulpa* from the Clytiinae (p. 70). The problem genus *Hypanthea* is discussed along with *Silicularia* (p. 50).

From the medusa stage, Kramp (1961) recognized only five genera World-wide: *Agastra, Eucopella*, *Gastroblasta*, *Obelia* and *Phialidium*; but of these only *Gastroblasta* and *Obelia* can now be recognized. Reference to discussions of these genera can be made using the index.

I have previously commented (Cornelius, 1975*a*) on the genera *Medusa* Linnaeus, 1758 (part); *Schizocladium* Allman, 1871; *Obelaria, Obeletta* & *Obelissa*, all Haeckel, 1879 (*Obelaria* Hartlaub, 1897, is a junior homonym and is discussed here under *Hautlaubella*); and *Monosklera* von Lendenfeld, 1885; all except the first of which fall into the synonymy of *Obelia* Péron & Lesueur, 1810*a*. I then mentioned also *Thaumantias* Eschscholtz, 1829, a junior subjective synonym of *Clytia* Lamouroux, 1812 (see below, p. 71). I overlooked (p. 254) that Mayer (1910: 262) had designated *Sertularia volubilis* sens. Ellis & Solander, 1786 (non Linnaeus, 1758) type species of *Clytia* (see p. 70 below). Lastly, I have reversed my opinion on the use of the genus name *Laomedea.*

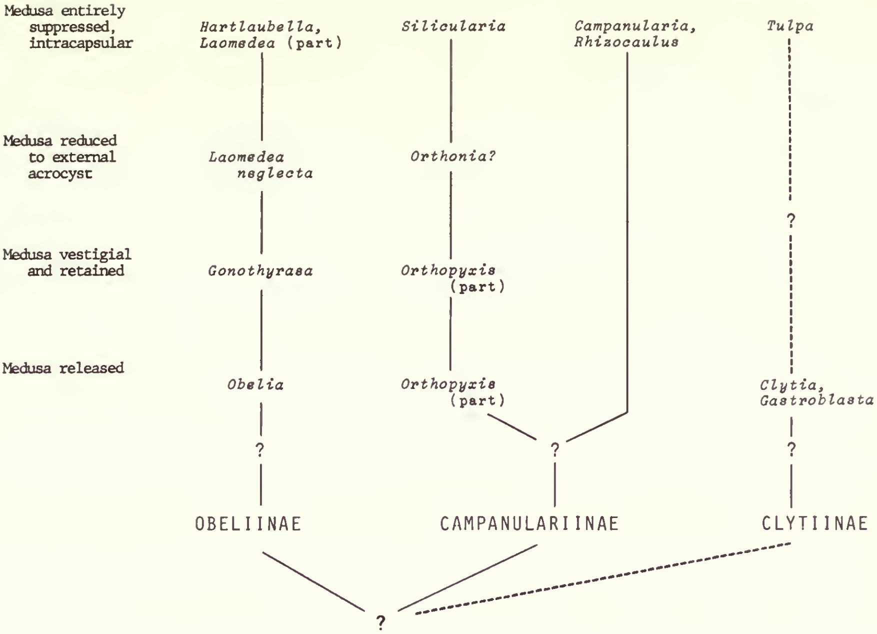

Medusa entirely suppressed, intracapsular
Medusa reduced to external acrocyst
Medusa vestigial and retained
Medusa released
Hartlaubella, Laomedea (part)
Laomedea neglecta
Gonothyraea
Obelia
Silicularia
Orthonia?
Orthopyxis (part)
Orthopyxis (part)
Campanularia, Rhizocaulus
Tulpa
Clytia, Gastroblasta
?
OBELIINAE
CAMPANULARIINAE
CLYTIINAE

Fig. 1 Affinities within the Campanulariidae. The genus *Eucalix* is not included since its method of reproduction is unknown, but vegetative characters suggest it is close to *Orthopyxis* (discussion on pp. 50–51). The diagram shows present-day similarities, not phylogenies, but the general direction of evolutionary advance is up the page and towards the right. Knowledge of the group is incomplete and the chart should be regarded as provisional.

Some of the species described herein are known only from either hydroid or medusa stages, and others were formerly so. Most species in which the two stages have been reconciled are now known by appropriate combinations, based on application of the International Code of Zoological Nomenclature; but those with incompletely known life-cycles cannot yet have their names confidently derived. Current knowledge in this family seems adequate for the Code to be applied to the two stages simultaneously, but this is arguably not so in all hydromedusan families and in some there may still be a case for retaining the dual system.

The subfamily divisions and their nomenclature

Although the limits of the family Campanulariidae have been agreed for nearly a century and a half (p. 47) only three authors (Haeckel, 1879; Mayer, 1910; Russell, 1953) have sought to group the genera into formal subfamilies. Indeed, until some quite recent studies of the range of reproductive structures found within the family had appeared (Miller, 1973; but also Splettstösser, 1924) interpretation and grouping had been difficult. Miller's important work showed that the structures which had once been called fixed gonophores in for example *Laomedea* spp. were vestigial, retained medusae; and that the curious externally-held 'meconidium' of *Gonothyraea loveni* is similarly to be regarded as a retained medusa.

Happily, this new interpretation of the dispersive generations (planulae and medusae) corroborates the broad divisions of the family based long ago solely on the vegetative characters of the hydroid stage (Broch, 1905, 1910; Goette, 1907; see p. 47, above). Hence the subfamily divisions adopted here, which draw on both groups of characters, might seem soundly based. But some problems remain and further refinement will no doubt be achieved when more is known of the non-European members of the family.

Subfamily **CAMPANULARIINAE**

Campanulariadae Johnston, 1836 : 107 (part).
Obelidae Haeckel, 1879 : 163 (part).
Obelinae: Mayer, 1910 : 231 (part).
Orthopyxinae Russell, 1953 : 303.
non Campanularinae: Russell, 1953 : 284 (=Clytiinae *nom. nov.*; see p. 69).

NOMENCLATURE. The spelling Campanulariinae takes as its root the genus name *Campanularia*, and Campanularinae is wrong.

DIAGNOSIS. Campanulariidae with colony usually reptant, secondarily erect and polysiphonic in *Rhizocaulus*; no true hydrothecal diaphragm; medusa absent except in *Orthopyxis*, where reduced.

TYPE GENUS. *Campanularia* Lamarck, 1816, the nominate genus.

SCOPE. The genera *Campanularia* Lamarck, 1816; *Silicularia* Meyen, 1834; *Orthopyxis* Agassiz, 1862; *Rhizocaulus* Stechow, 1919*b*; *Orthonia* Stechow, 1923*a*; and probably *Eucalix* Stechow, 1921*a*.

REMARKS. Of the included genera only *Campanularia, Orthopyxis* and *Rhizocaulus* are fully treated in this paper. The others have not been recorded from the eastern North Atlantic and are discussed only in this section.

Millard (1975 : 201) united *Campanularia* and *Orthopyxis* because she had seen *Orthopyxis* colonies having some unthickened hydrothecae; but I feel the remaining characters justify a separation.

The genus *Silicularia* Meyen, 1834, was proposed to include two species, *S. rosea* and *S. gracilis*, both being described as new. The early date of *Silicularia* and inadequacies in the descriptions of the two species make detailed comments necessary. The type species of *Silicularia* is *S. rosea*, designated by Stepanyants (1979 : 33). The species was based on Ethiopian and South African material. It was redescribed by Nutting (1915) and Stepanyants (1979), and Blanco (1967*a*) provided useful notes. The second species, *S. gracilis*, was based on infertile hydroid material from the Sargasso Sea and the Azores. It was probably a *Clytia* species. However, the figures and description do not include details of the hydrothecal rim or reproductive structures and I agree with Bedot (1905 : 171) that the species cannot be confidently assigned (see also p. 118). Nutting (1915 : 66) referred '*S. gracilis*' to the rather dubious species *Orthopyxis clytioides* (Lamouroux, in Freycinet, 1824, as *Tubularia*). He wrongly quoted Meyen as using the combination *Silicularia clytioides*. Meyen actually used *S. gracilis*. Rees & White (1966) made the same error when citing Meyen's Azores record. There seem no other reports of '*S. gracilis*' from the eastern North Atlantic. I provisionally refer *T. clytioides* Lamouroux to *Obelia dichotoma*, under which it is discussed further (p. 118). *S. gracilis* was mentioned recently by Stepanyants (1979), as *Campanularia.*

Nutting (1915), Bedot (1925), Broch (1929) and Stepanyants (1979) all regarded as congeneric with *Silicularia* the later genus *Hypanthea* Allman, 1876*a* (type species *H. repens* Allman, 1876*a*, by monotypy; type locality of the type species, Kerguelen I.), and I agree. *Hypanthia* Nutting, 1915 : 22, was a lapsus. Both Allman's (1876*a*, 1888) concept of *Hypanthea* and Nutting's and Stepanyants' of *Silicularia* included thick, asymmetrical hydrothecae, pedicels and stolons reminiscent of *Orthopyxis* Agassiz, 1862, to which the original concepts of the two genera come close. I have not located the type material of *H. repens*, but later material referred to *Hypanthea* species by Allman (1888) had an anastomosing stolon and other orthopyxine features.

So far as I can determine no *Silicularia* species has been recorded from the eastern North Atlantic. *S. atlantica* (Marktanner-Turneretscher, 1890, as *Hypanthea*), was based on material said to have come from 6° S, 38° W, but this position is on the mainland of South America!

The genus *Eucalix* Stechow, 1921*a* : 254, was proposed to accommodate the sole species

Campanularia retroflexa Allman, 1888, type locality Honolulu. Stechow maintained that the unusual hydrotheca of *E. retroflexus* justified generic separation. Both the type series (BMNH reg. no. 1888.11.13.14) and the original illustration (Allman, 1888 : pl. 11, figs 1, 1a) show the hydrothecal characters regarded important by Stechow. These characters, together with the anastomosing stolon of the type material, suggest that Stechow was justified in proposing the new genus. Millard (1957 : 196; 1975 : 212, as *Campanularia morgansi*) listed relevant literature. (I am grateful to Professor W. Vervoort for discussing the characters of this species; and to Dr D. M. Devaney for identifying the substrate of the type material. The substrate is a coralline alga, *Halimeda* sp., not a millepore as Allman stated. Dr Devaney informs me millepores have not been recorded from Hawaii.)

The genus *Orthonia* Stechow, 1923*a* : 94, 107, was proposed to accommodate a single orthopyxine species, *Campanularia everta* Clarke, 1876 : 253–254, pl. 39, fig. 4, type locality San Diego. Nutting had subsequently assigned to this species material having acrocysts and it was this character on which Stechow distinguished the genus from *Orthopyxis*. An element of subjectivity was thereby introduced since Stechow assumed that Nutting had material of the same species as had Clarke; and Stechow had no proof. Further revision of the orthopyxine species seems necessary before *Orthonia* is evaluated further.

Genus **CAMPANULARIA** Lamarck, 1816

Campanularia Lamarck, 1816 : 112 (part); Hincks, 1868 : 160 (part); Nutting, 1915 : 27 (part).
Campanula Westendorp, 1843 : 23 (lapsus pro *Campanularia*).
Campanulata Agassiz, 1862 : 354 (lapsus pro *Campanularia*).
Campanularia (*Eucampanularia*) Broch, 1910 : 184 (part).
Paracalix Stechow, 1923*c* : 3.

Type species. Provisionally to be taken as *Sertularia volubilis* Linnaeus, 1758 : 811 (*non* Ellis & Solander, 1786, see p. 70) as designated by Naumov (1960 : 249). Nutting (1915 : 28) earlier designated *S. verticillata* Linnaeus, 1758 : 811, as type species but application has been made to the International Commission on Zoological Nomenclature for this designation to be set aside (Cornelius, 1981; see Remarks). Broch (1905 : 10) proposed that '*Campanularia calyculata* Hincks, 1853' should be type species, but '*calyculata*' was not among the species originally included in the genus and so is not eligible. The correct spelling is of course *caliculata* (p. 65).

Diagnosis. Stoloniferous and colonial Campanulariidae, stolon not anastomosing; hydrothecae borne on pedicels inserted on the stolon at irregular intervals; true diaphragm absent; sub-hydrothecal spherule present; no medusa stage.

Remarks. The species *Sertularia verticillata* Linnaeus, 1758, was designated type species of *Campanularia* by Nutting (1915). But some authors, with whom I agree, have sought to remove *verticillata* to a distinct genus (Stechow, 1919*b*, *c*; Naumov, 1960, 1969). This would leave the name *Paracalix* Stechow, 1923*c*, available for the present genus; so that *Paracalix* would become applied for example to the common hydroids widely known as *Campanularia hincksii* (p. 53) and *C. volubilis* (auct.; p. 55). The genus *Paracalix* Stechow, 1923*c*, was proposed to accommodate only *Campanularia pulcratheca* Mulder & Trebilcock, 1914 : 11, pl. 2, figs 1–2, a species based on sterile material from Torquay, Victoria, Australia. (The generic name was actually misprinted *Cmpanularia* in Mulder & Trebilcock's heading.) The hydrotheca was sigmoid in lateral view and Stechow was impressed by the resulting bilateral symmetry. This was the main character on which the species, and subsequently Stechow's proposed genus, were based; but the specimen seems simply to have been a deformed specimen of *C. volubilis* or a closely related species. On this interpretation the species *pulcratheca* and the genus *Paracalix* are referred to *Campanularia*.

I have applied to the International Commission on Zoological Nomenclature for Nutting's designation of *S. verticillata* as type species of *Campanularia* to be set aside (Cornelius, 1981). If approved, this will validate Naumov's (1960) designation of *S. volubilis* Linnaeus, 1758, as type species of *Campanularia*. As a consequence the genus name *Rhizocaulus* Stechow, 1919*b*, can then be applied to the species *verticillata* (in the combination *R. verticillatus*, p. 67). See also the notes under *Rhizocaulus* (p. 67).

The subgenus *Eucampanularia* Broch, 1910, was introduced to embrace the five species *Sertularia volubilis* Linnaeus, 1758, *Campanularia integra* Macgillivray, 1842, *C. groenlandica* Levinsen, 1893, *C. speciosa* Clarke, 1877 and *S. verticillata* Linnaeus, 1758. The subgenus name has hardly been used in the literature. I designate *S. volubilis* Linnaeus, 1758, as its type species; so that *Eucampanularia* can be regarded a junior objective synonym of *Campanularia* (subject to my proposals to the ICZN being accepted; see also Cornelius, 1981).

Campanularia crenata Allman, 1876*b*

(Fig. 2)

Campanularia crenata Allman, 1876*b* : 258–259, pl. 11, figs 1–2.
Campanularia speciosus Clarke, 1877 : 210 (lapsus pro *speciosa*).
Campanularia speciosa (Clarke, 1877 : 214–215, pl. 9, fig. 11; Linko, 1911 : 185–187, fig. 34 (syn. *C. crenata* Allman); Broch, 1912*a* : 17–18, fig. 3; Nutting, 1915 : 48, pl. 8, fig. 5 (syn. *C. crenata* Allman); Broch, 1918 : 158–159 (syn. *C. magnifica* Fraser); Calder, 1970 : 1519, pl. 4, fig. 3.
Campanularia magnifica Fraser, 1913 : 164, pl. 11, figs 1–3.

NOMENCLATURE. The widely used trivial name *speciosa* was introduced in a paper published on 2 January, 1877, and not in 1876 as usually assumed. Hence *crenata*, genuinely introduced in 1876, has priority (see note on page 129 under Clarke, 1877).

The combination *Campanularia crenata* has been applied also to the species here called *Orthopyxis crenata*; but in that species the original binominal was *Eucopella crenata*, and primary homonymy has not occurred. There is secondary homonymy, however, and this is discussed under *O. crenata* (p. 60).

TYPE LOCALITY AND MATERIAL. Infertile colony on '*Thuiaria crassicaulis*' (Sertulariidae), ?Tsuger Straits, Japan, 183 m (100 fms); 1877.4.12.8 (previously unpublished data with specimen).

OTHER MATERIAL EXAMINED. All BMNH material is listed. 45 m, Store Hellefiskebanke, Greenland, fertile colony on *Sertularia mirabilis* (Verrill, 1873), coll. G. M. R. Levinsen, exch. Copenhagen Mus.; 1896.8.15.2 (Fig. 2; ?mentioned, Broch, 1918). 'Greenland', infertile colony on *Sertularia mirabilis*, ex D'Arcy Thompson colln, pres. Univ. Dundee; 1957.1.1.12. Infertile colony on *Sertularella* sp., Norman St, Labrador, Canada, ex D'Arcy Thompson colln, pres. Univ. Dundee; 1956.10.23.69. Infertile colony on *Symplectoscyphus* sp., Bell I, Newfoundland, Canada, 17 Apr 1892, ex D'Arcy Thompson colln, pres. Univ. Dundee; 1957.1.3.24. Infertile fragment, Bel Sund, Spitzbergen, 14 Jul 1898, 20 m, coll. Spetsberg Expedn, exch. Stockholm Mus.; 1960.8.29.33. No locality, fertile colony on sertulariid hydroid, exch. Copenhagen Mus.; 1912.12.21.44.

DESCRIPTION. Colony reptant. Stolon tortuous, branched, rugose. Hydrothecae on usually long pedicels, at irregular intervals; large, narrowest *c.* $\frac{1}{3}$ from rim, bulging out basally; rim much flared, with *c.* 10 rounded cusps, usually with striations running proximally from apex of each cusp; sub-hydrothecal spherule present; pedicel usually longer than hydrotheca, up to *c.* 3x length, spirally grooved throughout. Gonotheca ?♂ = ♀, elongate-ovoid, with or without long neck, borne on stolon.
Variation. The short necked gonotheca illustrated was apparently mature, indicating that the long necks usually regarded distinctive are not invariably present.

DISPERSIVE STAGE. Planulae, which develop within the gonotheca. Present material (1896.8.15.2) has just one in each gonotheca but there may have been more in life.

REPRODUCTIVE SEASON. No information.

DISTRIBUTION. A circumpolar Arctic Ocean and cold water species recorded in the Atlantic as far south as Newfoundland (present material), W Greenland and Spitzbergen (Broch, 1912*a*; Calder, 1970).

HABITAT. Usually reported epizoic on other hydroids. Naumov (1960, 1969) found an extreme depth range of 3 m to 600 m in Russian seas, most of his records being between 20 m and 200 m.

REMARKS. This species has been widely known by the combination *Campanularia speciosa*.

The long gonothecal neck often thought characteristic of the species is not present in all the material listed here, and is evidently variable in length.

Broch's (1918) attack on the validity of *Campanularia magnifica* Fraser, 1913, left no doubt that it is conspecific.

Campanularia hincksii Alder, 1856*a*
(Fig. 3)

Campanularia hincksii Alder, 1856*a* : 360, pl. 13, fig. 9; Hincks, 1868 : 162–163, pl. 24, fig. 3; Goette, 1907 : 189–193, pl. 15, figs 307–312; Broch, 1933 : 87–93 (syn. *C. alta* Stechow); Vervoort, 1946*a* : 276–277, fig. 122 (syn. *C. alta* Stechow); Patriti, 1970 : 33–34, fig. 41 (syn. *C. brachycaulis* Stechow, 1919*a*, here referred to *Clytia hemisphaerica*, see p. 82; *C. macrotheca* Leloup); Millard, 1975 : 208, fig. 67b–e.

Campanularia alta Stechow, 1919*a* : 54–57, fig. P.

Campanularia rara Stechow, 1919*a* : 60–61, fig. R.

Campanularia macrotheca Leloup, 1930*a* : 101–102, figs 1–3.

TYPE LOCALITY AND MATERIAL. Coast of Northumberland, England (Alder, 1856*a*; Millard, 1975). The syntype series is preserved jointly in the Hancock Museum, Newcastle upon Tyne, Northumberland (several colonies in spirit, epizoic on sertulariid hydroids) and the BMNH [small dry colony, 1857.8.3.58, epizoic on *Lafoea dumosa* (Fleming, 1820)]. It has been catalogued by Cornelius & Garfath (1980).

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia alta* Stechow, 1919*a*, infertile fragment of syntype on microslide, Naples; Munich Zoological Museum.

C. rara Stechow, 1919*a*, infertile fragment on microslide, Marseille; MZM.

OTHER MATERIAL EXAMINED. BMNH collection, *c*. 50 specimens. The following, collected by W. J. Rees, had fertile ♂ gonothecae: Hjeltefjord, nr Bergen, Norway, 40–90 m, 9 Apr 1962, 1962.10.7.20; I of Cumbrae, W Scotland, 90 m, 11 Jul 1966; 1967.12.1.10–12.

DESCRIPTION. Colony a tortuous stolon bearing unbranched hydrothecal pedicels at irregular intervals. Hydrotheca large, campanulate, truncate basally; length : breadth ratio variable (1·3–2·25 : 1, Millard, 1975); rim castellate, 8–15 blunt cusps each usually notched, occasionally deeply; main embayments deep, curved, often conspicuous, with characteristic folds trailing down from centres. Hydrothecal pedicel long, with spherule distally; shaft smooth to sinuous, usually with several annuli basally, sometimes also 1 – several annuli along length (Vervoort, 1946*a*). Hydranth ?undescribed, 18–24 tentacles visible in contracted BMNH material. Gonothecae ♂ = ♀, borne on stolon; sub-cylindrical, sometimes asymmetrical; broadest near base, truncate below, tapering gradually above; sides smooth to irregularly sinuous in a loose succession of rings; truncated and sometimes slightly flared distally; aperture wide, terminal; planula development probably internal; gonothecal pedicel short, ringed; colonies dioecious.

Variation. The BMNH series shows variation in the following features: size and length : breadth ratio of hydrotheca, height and number of cusps, depth of notch in cusps, presence or absence of longitudinal folds in hydrothecal wall; sinuosity of perisarc of hydrothecal pedicel, length of pedicel, number of basal annulations (may be absent), shape of proximal cavity in hydrotheca; sinuosity of gonothecal wall, amount of flaring below gonothecal aperture. Billard (1934) reported that the notch in the tips of the hydrothecal cusps may be absent, when the hydrothecae sometimes resemble those of *Campanularia volubilis* (p. 55).

DISPERSIVE STAGE. Planulae, which probably develop within the female gonotheca. Development of the male gonomedusoid was described by Goette (1907).

REPRODUCTIVE SEASON. Jun–Oct in NW France (Teissier, 1965). BMNH fertile material has collection dates within these limits except a male specimen from near Bergen, dated 9 Apr 1962.

DISTRIBUTION. Nearly cosmopolitan in shallow waters. Although not the most abundant hydroid *C. hincksii* can be expected almost throughout the eastern North Atlantic, local conditions permitting. Notable records include: N & S Iceland, Lofoten Is & Norway (Kramp, 1938); Mediterranean (Picard, 1958*b*); Italy (Rossi, 1971); Portugal (Da Cunha, 1950); Cap Spartel, Tangier & Cap Blanc, Morocco (Billard, 1907); Azores (Rees & White, 1966); Mauritania (Billard, 1931*a*); South Africa ('rare', Millard, 1975). The species is widespread in parts of temperate western Europe, including the British Isles (Hincks, 1868), but is scarce in Dutch and Belgian waters (Vervoort, 1946*a*; Leloup, 1952). There are several records from the Skagerrak and Kattegat (Kramp, 1935) and W Sweden (Jägerskiöld, 1971), but no records from the Baltic Sea (Stechow, 1927; Broch, 1928; Naumov, 1960, 1969) or Black Sea (Naumov).

HABITAT. Usually recorded between 20 m and 200 m but occasionally deeper: 'a few metres down to 800 m' (Kramp, 1938); 20–100 m, SW England (Marine Biological Association, 1957); *c.* 20 m, SW Wales (Crothers, 1966); 25–50 m, Scilly Is (Robins, 1969); below 20 m, NW France (Teissier, 1965); 112–120 m, Strait of Gibraltar & Morocco (Billard, 1907); 27–98 m, Azores (Rees & White, 1966); 86–210 m, southern Africa (Millard, 1975). Shallow records include: 15 m, NW Wales (Knight-Jones & Jones, 1956); 10–112 m, Faeroes (Kramp, 1929); 9·5–80 m, W Sweden (Jägerskiöld, 1971). Apparently no intertidal records.

The species seems unrecorded from brackish waters and may be stenohaline.

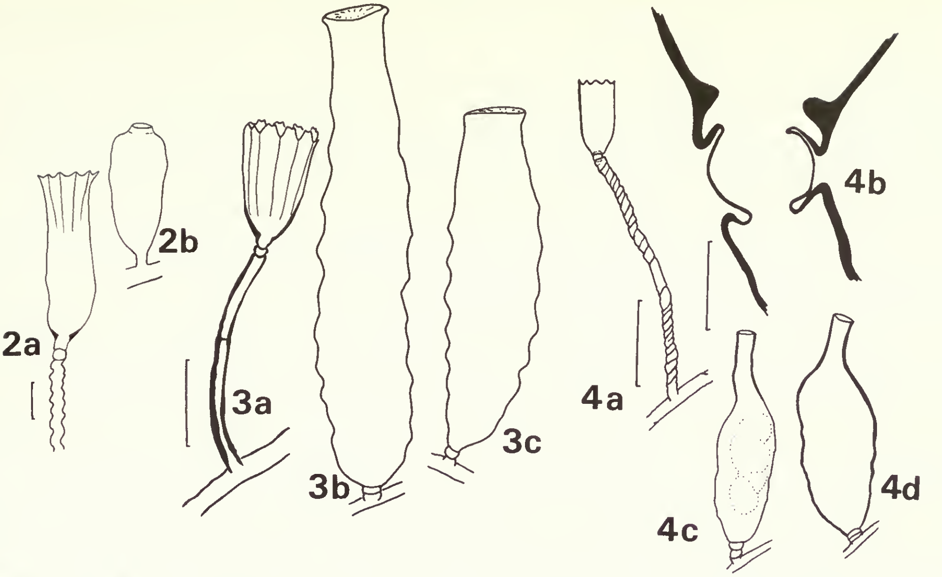
REMARKS. Millard (1975) summarized the doubts concerning the shape of the ♂ gonotheca, which it seems has not been reported before now. The BMNH series includes several colonies in which the gonothecal contents are preserved. The ♂ and ♀ gonothecae are identical, and are borne on separate colonies. The *contents* of the ♂ were described by Goette (1907) and are clearly gonomedusoid in Miller's (1973) terminology.

The name applied to the distinct but closely related nominal species *Campanularia laevis* Hartlaub (1905 : 565–567, pl. 1, based on Chile material) is a junior homonym of *Campanularia laevis* Couch, 1844 (see p. 65). I propose the name *Campanularia agas* nom. nov. for the Hartlaub species. *C. agas* was recently redescribed by Vervoort (1972 : 85–87, as *Campanularia laevis*). Both Hartlaub and Vervoort discussed similarities between *C. agas* (= *C. laevis* Hartlaub) and *C. hincksii*.

Hickson & Gravely (1907) referred additional material to '*C. laevis* Hartlaub', but Totton (1930) considered their material distinct. He referred it to a third nominal species, *Campanularia hicksoni* Totton, 1930. This was a species proposed to accommodate the material described by Hickson & Gravely, and also some collected by the 'Terra Nova'. It was discussed briefly by Rees & Thursfield (1965 : 90, as *Campanularia laevis* sensu Hickson & Gravely) and in detail by Stepanyants (1979 : 29).

Campanularia alta Stechow, 1919*a*, was based partly on new material from Villefranche and partly on some accounts of earlier authors. Stechow's material had young male gonothecae characteristic of *C. hincksii*, but he illustrated a hydrotheca more typical of *Clytia hemisphaerica*. However, the earlier descriptions included (i.e. those of Billard, 1907; Goette, 1907; Broch, 1912*b*) seem undisputedly of *C. hincksii*. Hence I concur with Broch (1933) and Vervoort (1946*a*) in regarding *C. alta* conspecific, and not with Picard (1951*a*, 1955) who maintained it distinct.

Campanularia macrotheca Leloup, 1930*a*, based on material from Monaco, was justifiably referred to the present species by Patriti (1970).



Figs 2–4 **Fig. 2** *Campanularia crenata.* (a) hydrotheca and (b) ♀ gonotheca, Greenland, 1896.8.15.2. Scale 500 μm. **Fig. 3** *Campanularia hincksii.* (a) hydrothecal pedicel and part of stolon. The pedicel is unusually short for the species. Note the irregular thickening. W Norway, 30–40 m. (b) ♀ and (c) ♂ gonothecae, sexes identified from contents. W Scotland, 90 m, July 1966; 1967.12.1.16 and .10 respectively. The ♀ gonotheca is unusually long. Scale (a–c) 500 μm. **Fig. 4** *Campanularia volubilis.* (a) hydrotheca and pedicel, 30–40 m, nr Bergen, 15 August 1962; 1962.11.7.6. Scale 500 μm. (b) vertical optical section through (a), showing flexible region. Scale 50 μm. (c–d) two gonothecae, one with ova, from a single colony, Shetland; 1912.12.21.55. Scale as (a).

Campanularia volubilis (Linnaeus, 1758)
(Fig. 4)

Corallina minima scandens, vesiculas campaniformes in summo caule lineari contorto gerens. Ellis, 1755 : 24–25, pl. 14, figs A, a.

Sertularia volubilis Linnaeus, 1758 : 811; Linnaeus, 1767 : 1311; (*non* Pallas, 1766 : 122, junior homonym, = *Calycella syringa* (Linnaeus, 1767), see also Cornelius, 1978; *non* Ellis & Solander, 1786 : 51, pl. 4, figs E, e, F, f, = *Clytia hemisphaerica*, see p. 70).

Sertularia uniflora Pallas, 1766 : 121–122 (nom. nov. pro *S. volubilis* Linnaeus, 1758; see pp. 77–78); (non Ellis, 1768 : 434, pl. 19, fig. 9, = *Clytia hemisphaerica*, see p. 78).

Campanularia volubilis: Alder, 1857 : 125–126, pl. 4, fig. 7; Hincks, 1868 : 160–162, pl. 24, fig. 2 (non Hincks, 1852, nec Du Plessis, 1871, = *Clytia hemisphaerica,* see p. 70).

Campanularia groenlandica Levinsen, 1893 : 168, pl. 5, figs 10–12; Naumov, 1960 : 252–253, fig. 139; Naumov, 1969 : 273–274, fig. 139; see Remarks.

non *Clytia volubilis:* Hargitt, 1909 : 373–374 (= *C. hemisphaerica*, see p. 78).

Clytia mollis Stechow, 1919*a* : 44–45, fig. L (?syn. *Clytia laevis* Weismann, 1883).

Campanularia brachycaulis Stechow, 1919*a* : 62–63, fig. T.

NOMENCLATURE. Further synonymies were given by Bedot (1901–1925), Vervoort (1946*a*) and Naumov (1960, 1969) among others.

TYPE MATERIAL AND LOCALITY. Linnaeus (1758) gave only Ellis' (1755) illustration as indication. As with some other hydroids (Cornelius, 1979 : 309, notes 11–14) Linnaeus apparently based the designation on Ellis' plate and not on specimens. Almost certainly the material now in the Linnaeus collection in the Linnean Society of London (Savage, 1945 : 206) reached Linnaeus after the original description was published and cannot be regarded as type (Cornelius, 1975*a* : 273, footnote). The material collected and described by Ellis [infertile colony on *Hydrallmania falcata* (Linnaeus, 1758); Brighton, Sussex, England, June, 1754; illustrated, Ellis, 1755 : pl. 14, figs A, a] can thus be considered type. Although some hydroid material of John Ellis survived until recently it seems that only a single specimen (of *Nemertesia* sp.) escaped destruction during World War II (Cornelius, 1975*a* : 267, footnote) and the specimen illustrated by Ellis can be assumed lost. The type locality is Brighton.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia groenlandica* Levinsen, 1893, infertile syntype material on two pieces of *Lafoea dumosa* (Fleming, 1820), in spirit, exch. Copenhagen Mus., Davis Strait, '80 fms'; 1896.8.15.1.

Campanularia brachycaulis Stechow, 1919*a*, infertile fragments on 2 microslides, Villefranche; Munich Zoological Mus.

Clytia mollis Stechow, 1919*a*, small fertile colony on weed, Sète, S France; MZM.

OTHER MATERIAL EXAMINED. BMNH collection, *c*. 60 specimens.

DESCRIPTION. Colony comprising creeping stolon bearing irregularly spaced, erect, straight pedicels each supporting a hydrotheca. Stolon smooth to irregularly spirally grooved. Pedicels apparently always unbranched, smooth to spirally grooved throughout; subhydrothecal spherule present. Hydrotheca tubular, tapering abruptly basally; rim with 10–12 shallow blunt cusps; sometimes with fine longitudinal striae associated with the cusps. Gonothecae scarce, ♂ = ♀, on short pedicels; flask-shaped, smooth, aperture at end of neck of indefinite length; neck forms after body of gonotheca; on stolon or (Hincks, 1868) on hydrothecal pedicels.

DISPERSIVE STAGE. Planulae, brooded in the ♀ gonotheca. There is no medusa stage.

REPRODUCTIVE SEASON. Apparently the only published information is of a fertile specimen off Norfolk, 16 June, 1951 (Hamond, 1957). None of the dated specimens in the BMNH is fertile. Possibly reproduction in this species is usually vegetative. Hamond found fertile material just once, and only a few of the BMNH specimens have gonothecae.

DISTRIBUTION. Common from southern England northwards, but probably present in scattered localities further south. Not recorded from NW France or Belgium, nor reliably from the Netherlands (Teissier, 1965; Leloup, 1952; Vervoort, 1946*a*). However, the species is well known from the south coast of England (Ellis, 1755; Marine Biological Association, 1957). Vervoort (1949) recorded a single specimen from the Channel Isles but was 'unable to trace records along the NW coast of France'. There are some records from the Mediterranean Sea (Stechow, 1923*a*; Riedl, 1959; Naumov, 1969) but Picard (1958*b*) excluded the species from his faunal list. There is a record from N Spain (Santander; Rioja y Martín, 1906) and another from Mauritania (Billard, 1931*a*); but in general there are few records further south than the British Isles.

Northerly records include: Iceland, numerous examples (Kramp, 1938); Greenland, widespread up to 72° N (Kramp, 1943); N Norway and N coast of Russia (Mathiesen, 1928; and Naumov, 1969, as *C. groenlandica*).

HABITAT. Both Mathiesen (1928, N Norway) and Naumov (1969, Russian seas) reported a usual depth range of 25–100 m, Naumov giving extreme limits of 5–250 m. Kramp (1943, Greenland) gave a range of 25–650 m.

Hincks (1868) stated the substrate to be other hydroids. All the BMNH material is on hydroids, especially *Tubularia larynx* (sens. auct., e.g. Hincks, 1868), *Hydrallmania falcata* (Linnaeus, 1758) and *Abietinaria abietina* (Linnaeus, 1758), and other sertulariids. Although Couch (1844) reported material on the antennae of crabs and on a bivalve (*Pinna fragilis*, as '*P. ingens*'), his description of the gonotheca suggests his material was *Clytia hemisphaerica*. He evidently confused the two species.

REMARKS. Some nomenclatural confusion between the present species and *Sertularia uniflora* Pallas, 1766, is discussed below (pp. 77–78).

Rees & Thursfield (1965) suggested that *C. volubilis* might prove conspecific with *Rhizocaulus verticillatus* (p. 67). Their evidence was some similarity in the hydrothecae and gonothecae of the two species. However, the long BMNH series confirms the several constant differences. The linear dimensions of hydrothecae, hydrothecal pedicels, gonothecae and stolon diameters in *C. volubilis* are about half the same dimensions in *R. verticillatus*. And while none of the *C. volubilis* specimens has polysiphonic, erect stems these are present in all the *R. verticillatus* specimens. There is no intermediate material. Further, the perisarc tubes in *R. verticillatus* are nearly all parallel. Had the two forms been conspecific, colonies of *C. volubilis* s. str. with some aggregation of the perisarc tubes might have been found; but there are no such specimens in the BMNH series.

As noted by Hincks (1868) the distinction between *C. volubilis* and the hydroid stage of *Clytia hemisphaerica* was overlooked by Johnston (1847), but recognized soon afterwards by Alder (1857). Couch (1844) also confused the two.

Confusion between *C. volubilis* and the species now called *Calycella syringa* (Linnaeus, 1767) occurred in the mid-eighteenth century but was resolved by Linnaeus (1767) himself. Essential details are given in the above synonymy, and further discussion in Cornelius (1978). The species is currently referred to the family Campanulinidae.

Campanularia groenlandica Levinsen, 1893, although widely recognized, was apparently founded on *C. volubilis* material from the Davis Strait. Syntype material in the BMNH shows features present in the original illustrations of *groenlandica*, for example spirally sculptured hydrothecal pedicels and blunt cusps on the hydrothecal rim; and the gonotheca shown in the original illustration is identical with that normal in *C. volubilis*. Thus the two taxa appear conspecific. Material has been recorded as *C. groenlandica* from Trondheim Fjord (Mathiesen, 1928) north to 68° 20′ N (Kramp, 1943; 50–525 m depth); and Naumov (1969) recorded '*C. groenlandica*' from the N coast of Russia.

The type material of *Clytia mollis* Stechow, 1919*a*, examined here, comprises immature colonies of *C. volubilis*. Stechow's original illustration incorrectly shows a truncate, wide mouthed gonotheca. It is simply a young one in which the long neck has yet to form. The hydrothecal pedicels illustrated are topped by sub-hydrothecal spherules not present in *Clytia*. Stechow tentatively included in the synonymy of '*C. mollis*' the nominal species *Clytia laevis* Weismann, 1883, based on Naples material. However it is clear from Weismann's description that *C. laevis* was founded on normal *Clytia hemisphaerica* material, and it is here referred to that species.

Genus ***ORTHOPYXIS*** Agassiz, 1862

Clytia: Westendorp, 1843 : 23 (part; see Remarks under *Orthopyxis integra*).
?*Silicularia* Meyen, 1834 : 206 (?part; see Remarks and p. 50).
Campanularia: Macgillivray, 1842 : 465 (part); Couch, 1844 : 40 (part); Hincks, 1868 : 160 (part); Millard, 1975 : 203 (part); (see Remarks below, and under *O. integra*).
Clytia (*Orthopyxis*) Agassiz, 1862 : 297.
Clythia Agassiz, 1862 : pl. 28 (lapsus for *Clytia*).
Orthopyxis Agassiz, 1862 : 355; Ralph, 1957 : 834; Arai & Brinckmann-Voss, 1980 : 101.
Hincksia Agassiz, 1862 : 355 (sic).
Eucopella von Lendenfeld, 1883*a* : 188.
Agastra Hartlaub, 1897 : 452 (nom. nud.), 504; Kramp, 1961 : 160.
Leptomedusa Browne, 1900 : 714 (see notes on Nomenclature under *O. integra*).

TYPE SPECIES. *Clytia* (*Orthopyxis*) *poterium* Agassiz, 1862; by monotypy; may be conspecific with *O. integra*. *Orthopyxis* was introduced by Agassiz as a subgenus of *Clytia* on page 297 of his work, comprising the 'new' species *poterium* alone; but on page 355 he upgraded it to genus. On that page he implicitly used the combinations '*Orthopyxis* (*Orthopyxis*) *poterium*', '*Orthopyxis* (*Campanularia*) *volubiliformis*' and '*Orthopyxis* (*Laomedea*) *integra*' (of various authors). Thus *poterium* should rightly be taken as type species by monotypy of the subgenus *Orthopyxis* Agassiz, 1862. Nutting's (1915 : 63) designation of *Campanularia caliculata* Hincks, 1853, as type species must be disregarded since *caliculata* was not originally included. It was unfortunately repeated by Arai & Brinckmann-Voss (1980).

DIAGNOSIS. Campanulariidae forming stoloniferous or short unbranched upright colonies; stolon anastomosing; true diaphragm absent; hydrotheca fundamentally radially symmetrical but often asymmetrically thickened; medusa reduced, lacking manubrium and tentacles, not feeding, believed facultatively retained in at least one species.

REMARKS. The genera *Silicularia* Meyen, 1834, and *Hypanthea* Allman, 1876*a*, are discussed on page 50.

Ralph (1957) listed some works in which *Orthopyxis* was discussed in relation to *Eucopella* von Lendenfeld, 1883*a* (based partly on *Campanularia bilabiata* Coughtrey, 1875); and other discussion was provided for example by Bale (1914), Nutting (1915) and Fraser (1918). The species *Eucopella campanularia* was described in greater detail in another paper (von Lendenfeld, 1883*b*). Bale, Ralph and others referred *Eucopella* to *Orthopyxis*; but Hirohito (1969) held the two genera distinct on the presence or absence respectively of marginal vesicles in the (retained) 'eumedusoid'. He referred *caliculata* Hincks, 1853, to *Eucopella*, stating an intention to discuss the generic question later. However, *caliculata* is here referred to *O. integra*; and generic separation seems unjustified. I provisionally follow several previous authors in regarding *Eucopella* congeneric. However, Kramp (1961) accepted the genus and included in it the two species *bilabiata* Coughtrey, 1875, and *crenata* Hartlaub, 1901. He designated *bilabiata* type species. The two species Kramp included may not be distinct: they are treated here under *O. crenata* (p. 60). Kramp's generic separation, from the 'medusa' genus *Agastra*, was based on minor differences in the medusa and is not upheld here.

The genus *Hincksia* Agassiz, 1862, was proposed to accommodate solely the well described species *Campanularia tincta* Hincks, 1861*a*; but Bedot (1910 : 311), Stechow (1923*a* : 94) and Rees & Thursfield (1965 : 93) referred the genus to *Campanularia* auct. In proposing the genus Agassiz stated merely 'The genus *Hincksia* is characterized by its one-sided, ringled, fertile hydra', hardly an acceptable diagnosis. Nevertheless, type material of *C. tincta* is available (BMNH reg. no. 1899.5.1.219–220), as noted by Rees & Thursfield. Although dry the material shows the characters of the genus *Orthopyxis* Agassiz, 1862, and *Hincksia* and *Orthopyxis* (not *Campanularia*) can be regarded congeneric. Under the first reviser principle I retain *Orthopyxis*, which has been widely used, and suppress *Hincksia*, which has not. *O. tincta* is an Australian species and so is outside the present scope, but it may be noted in passing that the type material has an anastomosing stolon like *Orthopyxis* s. str. and a highly distinctive, closely ringed gonotheca. Useful synonymies of the species were provided by Nutting (1915), Stechow (1923*a*) and Rees & Thursfield (1965), and a redescription by Stepanyants (1979). *Campanularia tincta* sensu Warren, 1908, is mentioned here under *C. africana* Stechow, 1923*d*, a junior synonym of *O. crenata* (p. 60).

The genus *Agastra* Hartlaub, 1897, was based on Helgoland material of the medusa stage of *Orthopyxis integra* (see also p. 67). Kramp (1961) resurrected the genus but there seems no doubt that its synonymy with *Orthopyxis* is justified.

Orthopyxis crenata (Hartlaub, 1901)
(Fig. 5)

?*Campanularia bilabiata* Coughtrey, 1875 : 291–292, pl. 20, figs 46–49.
?*Campanularia everta* Clarke, 1876 : 251, 253–254, pl. 39, fig. 4; Garcia Corrales *et al.*, 1978 : 24–25, fig. 9 (syn. *C. lennoxensis* Jaderholm).
Eucopella crenata Hartlaub, 1901 : 364–366, pl. 22, figs 27–31, 33–35; Hirohito, 1969 : 7, fig. 7.
?*Campanularia lennoxensis* Jaderholm, 1904*b* : 268–269, pl. 12, figs 4–5.
Campanularia ?intermedia Stechow, 1919*a* : 66–68, fig. V.
?*Orthopyxis delicata* Trebilcock, 1928 : 3, pl. 2, fig. 1; Garcia Corrales *et al.*, 1978 : 22–23, fig. 8.

Campanularia crenata forma *intermedia:* Picard, 1951*a* : 345.
Campanularia crenata: Picard, 1955 : 186; Millard & Bouillon, 1973 : 47–48, fig. 6B–F; Millard, 1975 : 204–206, fig. 68A–F (?syn. *Orthopyxis delicata* Trebilcock, 1928); Garcia Corrales *et al.*, 1978 : 19–22, fig. 7; (non Allman, 1876*b*).
Orthopyxis crenata: Trebilcock, 1928 : 3; Ralph, 1957 : 838–840, fig. 6g–v (syn. *O. formosa* Trebilcock, 1928); Rees & Thursfield, 1965 : 104.

Type material and locality. The species was based partly on material from French Pass, Bare Island, New Zealand, and partly on the original description of *Campanularia bilabiata* Coughtrey, 1875. I have located none of the type material. Ralph (1957) restricted the type locality to French Pass.

Material examined. I have seen no Atlantic material of this species.

Description and identification of hydroid stage. The lack of available material of this species and the taxonomic confusion surrounding the whole genus together make redescription difficult. The following identification notes are adapted from Ralph (1957), Millard & Bouillon (1973) and Millard (1975). Differing from *O. integra* as follows: hydrothecal rims smooth through gently wavy to crenate, with 8–12 short rounded cusps, commonly varying within a colony (always smooth in *O. integra*); hydranth with *c.* 14 tentacles (> 20 in *O. integra*: Ralph, 1957; but see p. 40). Other reported differences seem invalid (but see Dispersive stage).

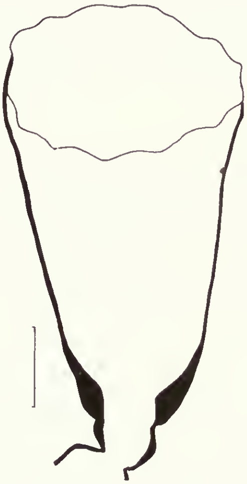


Fig. 5 *Orthopyxis crenata.* Hydrotheca, Port Phillip, Australia, intertidal; 1959.10.1.1. Scale 10 μm.

Variation. Ralph (1957) and Millard (1975) indicated that the variation in *O. crenata* parallels that in *O. integra* (p. 63).

Dispersive stage. A medusa. By homology with *O. integra* it might be expected that the medusa is short lived and does not feed. Hirohito (1969) described newly released medusae. The umbrella was sub-spherical (0·5 mm high, 0·6 mm wide). There was a distinct velum, 4 broad radial canals and 8 statocysts; but no tentacles or stomach. Published descriptions suggest that the medusa of *O. integra* differs in being proportionately taller.

Reproductive season. Fertile material recorded early March near Marseille (Stechow, 1919*a*).

Distribution. From N coast of Spain (Garcia Corrales *et al.*, 1978, as *Campanularia everta*) and Mediterranean Sea southwards (S France, Stechow, 1919*a* as *C. intermedia*; Picard, 1951*a*, 1958*b*; Millard, 1975; Algeria, Picard, 1955; S Spain, Garcia Corrales *et al.*). Widely distributed in warmer parts of all oceans (Millard). Cape Verde Islands (Rees & Thursfield, 1965).

HABITAT. On *Posidonia* (eel grass) and Bryozoa (Millard & Bouillon, 1973, Seychelles); intertidal to about 3 m (Millard, 1975, southern Africa); 1–20 m, Spain (Garcia Corrales *et al.*, 1978). *Campanularia africana* sens. Buchanan (1957), possibly conspecific, came from 14 m off Ghana (see Remarks).

REMARKS. Authors who have placed this species in the genus *Campanularia* have apparently overlooked the senior homonym *Campanularia crenata* Allman, 1876*b* (see p. 52). If the present species is again referred to *Campanularia* another specific name would be required, and one of the names discussed by Hartlaub (1901) might be available.

Hartlaub thought *O. crenata* (Hartlaub) close to *Eucopella campanularia* von Lendenfeld, 1883*a*, *b*, and 'identical with' *Campanularia bilabiata* Coughtrey, 1875. Ralph (1957), however, treated '*Orthopyxis crenata*' and '*Silicularia bilabiata*' under different genera. In this Ralph was unwise since *crenata* Hartlaub was, in part, a nom. nov. for *bilabiata*. The name *bilabiata* might prove to be available for the present species but to avoid further confusion *crenata* is retained pending a review of the whole genus. See also the notes on *Eucopella* (p. 58).

Picard (1958*b*) recorded the nominal species *Orthopyxis everta* (Clarke, 1876, as *Campanularia*, based on Californian material) from 'the Mediterranean'. The original description resembles the present species, and the two might prove conspecific; but I have seen type material of neither. Ralph (1957) separated them on the structure of the gonotheca. If a synonymy were propsed *everta* might take priority for the present species but *C. bilabiata* Coughtrey is still older. Vervoort (1972 : 87) redescribed '*O. everta*' recently and gave further synonymy.

The nominal species *Campanularia ?intermedia* Stechow, 1919*a*, was based on material from Marseille. I have not located type material but the vegetative characters given in the description seem identical with those of the present species as currently understood. As suggested by Stechow, and also by Garcia Corrales *et al.* (1978), *C. lennoxensis* Jaderholm, 1904*b*, is probably conspecific.

Campanularia africana Stechow (1923*d* : 104, nom. nov. pro *C. tincta* sensu Warren, 1908, from Natal; non *C. tincta* Hincks, 1861a, from 'Australia', see p. 58) was recorded from Takoradi, Ghana at 14 m depth by Buchanan (1957). *O. africana* has been distinguished from *O. crenata* by Millard (1975), who redescribed both, mainly on gonothecal characters; and from the several reportedly endemic South African species she recognized on variations in these characters alone. However, the relatively poor original descriptions of most of the nominal species and the general taxonomic confusion in the genus make it unwise to accept Buchanan's record without further evidence. It is the only record of *O. africana* from north of the equator.

Discussion of the non-Atlantic nominal species of *Orthopyxis* having crenate hydrothecal margins was provided by Ralph (1957).

Millard (1975) provisionally referred *Orthopyxis delicata* Trebilcock, 1928, to the present species; and it seems likely that *O. delicata* sensu Garcia Corrales *et al.* (1978; N & S Spain) is similar.

Orthopyxis integra (Macgillivray, 1842)

(Fig. 6)

?*Clytia undulata* Lamouroux, in Freycinet, 1824 : 617–618, pl. 94, figs 4–5.

Campanularia integra Macgillivray, 1842 : 465; Johnston, 1847 : 109, pl. 28, fig. 2 (syn. *C. laevis:* Saunders, in Johnston, 1847); Hincks, 1868 : 163–164, pl. 31, fig. 1; Levinsen, 1893 : 168–169, pl. 5, figs 14–18 (syn. *C. caliculata* Hincks; *C. gracilis* Allman, 1876*b*); Broch, 1918 : 159–162 (syn. *C. compressa* Clarke; *C. ritteri* Nutting, 1901*a*); Vervoort, 1946*a* : 274–276, figs 120–121 (syn. *C. laevis* Couch; *C. caliculata* Hincks; *C. breviscyphia* Sars; *Clytia* (*Orthopyxis*) *poterium* Agassiz; *Laomedea repens* Allman); Millard, 1975 : 208–211, fig. 69 (syn. *C. caliculata* Hincks; *C.*

compressa Clarke; *Agastra mira* Hartlaub; *Agastra rubra* Behner; *?Campanularia gracilis:* Stechow, 1925).

Clytia ryckholtii Westendorp, 1843 : 23–24, pl. 1, figs e, f.

Campanularia laevis Couch, 1844 : 42; Gosse, 1855 : 25; (non *C. laevis* Hartlaub, 1905 = junior homonym).

Capsularia integra: Gray, 1848 : 86 (?syn. *Campanularia laevis* Couch).

Capsularia laevis: Gray, 1848 : 87.

Campanularia caliculata Hincks, 1853 : 178–179, pl. 5, fig. B; Hincks, 1868 : 164–167, pl. 31, fig. 2 (syn. *C. breviscyphia* Sars; *Clytia* (*Orthopyxis*) *poterium* Agassiz.

Campanularia breviscyphia Sars, 1857 : 158–159, pl. 1, figs 12–13.

Clytia (Orthopyxis) poterium Agassiz, 1862 : 297–304.

Clythia poterium Agassiz, 1862 : pl. 28, figs 1–20, pl. 29, figs 1–5.

Orthopyxis poterium Agassiz, 1862 : 355.

Clytia posterior Wright, 1862 : 308 (lapsus pro *poterium* Agassiz).

Laomedea repens Allman, 1871 : 49, fig. 20.

?Eucopella campanularia von Lendenfeld, 1883*a* : 186–189.

Campanularia compressa Clarke, 1877 : 214, pl. 8, figs 5–6; Patriti, 1970 : 34–35, fig. 43 (syn. *C. platycarpa* Bale).

Campanularia borealis Marktanner-Turneretscher, 1890 : 206.

Campanularia integriformis Marktanner-Turneretscher, 1890 : 207, pl. 3, fig. 2.

'A leptomedusan' Browne, 1897 : 832, pl. 49, figs 3, 3a.

Agastra mira Hartlaub, 1897 : 452, 504–506, pl. 22, figs 5, 8–10; Mayer, 1910 : 234 (syn. *Campanularia caliculata* Hincks); Russell, 1953 : 303–306, pl. 19, fig. 1, text-figs 186–188 (syn. '*Leptomedusa* sp.' Browne; *Campanularia caliculata* Hincks).

Agastra caliculata: Browne, 1900 : 714–715 (syn. *A. mira* Hartlaub; *Leptomedusa* Browne).

Leptomedusa gen.? sp.? Browne, 1900 : 714.

Campanularia calyculata: Goette, 1907 : 193–204, pl. 15, figs 313–325 (syn. *Clytia poterium* Agassiz).

?Agastra rubra Behner, 1914 : 393–398, pl. 7, fig. 6, text-figs 8–10.

Orthopyxis compressa: Stechow, 1919*a* : 69, fig. Wa–b; Picard, 1951*b* : 110; Picard, 1958*a* : 2.

Orthopyxis asymmetrica Stechow, 1919*a* : 71–72, fig. Xa–e.

Clytia rijckholtii Leloup, 1947 : 22 (unjust. emend. pro *C. ryckholtii* Westendorp).

Orthopyxis caliculata: Ralph, 1957 : 838, text-figs 6a–f (syn. *O. macrogona* von Lendenfeld); Picard, 1958*b* : 191 (syn. *Campanularia integriformis* auct.; see Remarks).

Orthopyxis integra: Rees & Thursfield, 1965 : 103–104.

Eucopella caliculata: Hirohito, 1969 : 6–7, fig. 6.

NOMENCLATURE. An unjustified emendation of the nominal species name *caliculata*, to *calyculata*, was followed by several authors (listed in Bedot, 1918, 1925).

Browne (1897) described the medusa of the present species but did not identify it, calling it simply 'A Leptomedusa gen.? sp.?'. Evidently Browne did not then regard Leptomedusa a generic name; but he later (Browne, 1900) used it thus: '*Leptomedusa* gen.? sp.?', in a formal synonymy under '*Agastra caliculata* (Hincks, 1853)'. Nevertheless it seems in keeping with Browne's intentions not to regard *Leptomedusa* as part of nomenclature.

The widely used species name *integra* may prove to be threatened by an older but obscure name, *undulata*.

TYPE LOCALITY AND MATERIAL. Mouth of River Don, Aberdeen, Scotland; on *Tubularia indivisa* Linnaeus, 1758; material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia laevis* Couch, 1844, neotype, proposed herein.

Campanularia caliculata Hincks, 1853, colony on *Laminaria* sp. and the red alga *Phycodrys rubens* (L.) Batt. (det. J. H. Price), in spirit, nr Old Head of Kinsale, Co Cork, Eire, coll. R. Allman, syntype; 1853.4.7.16. Remainder of type series, from Pegwell Bay, E. Kent, England, coll. R. S. Boswell, not located. The type locality of *C. caliculata* was restricted to Pegwell Bay by Ralph (1957) but the Co Cork material remains part of the syntype series.

Orthopyxis asymmetrica Stechow, 1919*a*, infertile material on 2 microslides, Marseille; Munich Zoological Museum.

OTHER MATERIAL EXAMINED. BMNH collection, *c.* 50 specimens, mostly from the British Isles.

DESCRIPTION OF HYDROID STAGE. Colony a creeping hydrorhiza with single, irregularly spaced hydranths and hydrothecae on long pedicels and, separately, subsessile gonophores and gonothecae. Hydrorhiza smooth but sinuous, walls almost unthickened but often (Ralph, 1957; Millard, 1975) with a flat lateral flange of perisarc; branched frequently and (e.g. BMNH 1922.3.6.170, 1962.11.7.9) occasionally anastomosing. Hydrothecal pedicels usually narrower than hydrorhiza; walls usually much thickened; typically grooved with a smooth spiral; often 2–3 widely spaced shallow annuli near top; sub-hydrothecal spherule present; hydrotheca cup-shaped, length : breadth ratio variable; base wide to narrow, walls almost straight and diverging in narrower-based specimens; often flared near rim; walls thin to very thick, but rim region almost always unthickened; amount of thickening varying between adjacent hydrothecae and within a single hydrotheca (Fig. 6); rim even; small spherical chamber formed basally within hydrotheca by internal ring of perisarc. Hydranth with 20–30 tentacles (histological details in Agassiz, 1862; Stefani, 1956, 1959; Kawaguti, 1966; anatomical details of a possibly conspecific form in von Lendenfeld, 1883*b*). Gonotheca ♂ = ♀; broad, roughly parallel sided; truncated and slightly narrowing above, tapering more or less abruptly below; length usually 1½–2x breadth, occasionally 5–6x (e.g. Allman, 1871 : fig. 20, as *Laomedea repens*; Vervoort, 1946*a* : fig. 120); usually laterally flattened but sometimes circular in transverse section; walls of gonotheca often thickened, sometimes much so; smooth through sinuous to deeply grooved spirally; aperture distal,

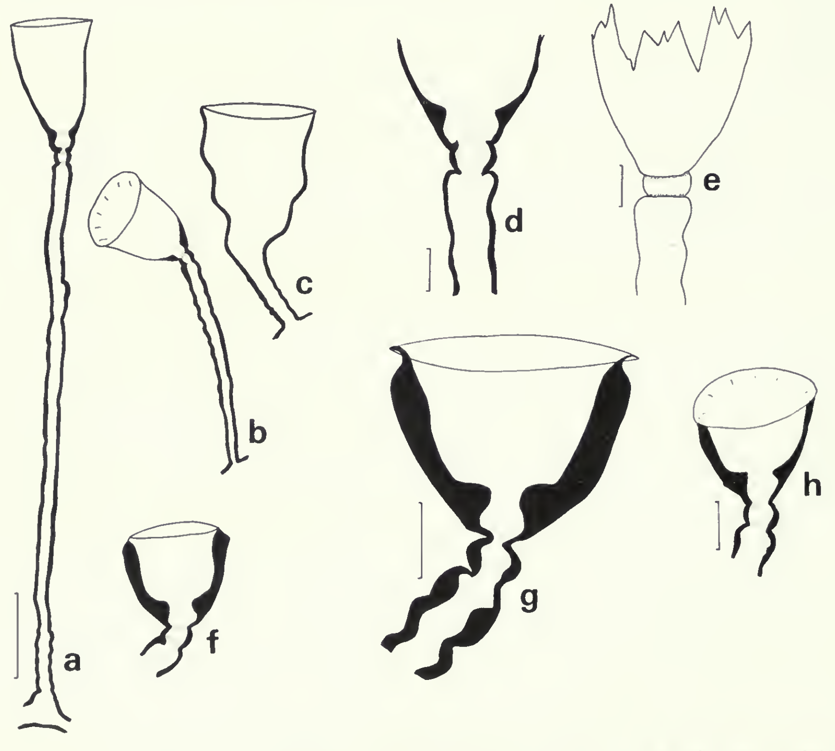


Fig. 6 *Orthopyxis integra.* (a–e) 15–25 m, Espegrend, W Norway, 13 April 1962; 1962.10.7.11. (a–b) adjacent hydrothecae with differing pedicel lengths. (c) gonotheca, sex unknown. (d–e) sub-hydrothecal spherule. (f–h) Knysna, Cape Province, Republic of South Africa, 1922.3.6.170. Scales: (a–c, f) 500 μm; (d–e) 10 μm; (g) 10 μm; (h) 10 μm.

nearly as wide as maximum diameter of gonotheca. Pedicel short to absent, usually unringed and grading into base of gonotheca (but see Fig. 6). Blastostyle with one well developed medusa, whether retained or released, and a second basal bud the fate of which seems unrecorded (see Dispersive stage). Present evidence suggets that medusae of either sex are sometimes retained. Nematocysts described by Östman (1979).

Variation in hydroid stage. See also the comments of Ralph (1957 : 838) and Millard (1975 : 209). Even among the Campanulariidae *O. integra* is unusually variable in morphology, and is unusual also in its habit of sometimes releasing and at other times retaining the medusa. Some of the variation may be genotypic, but the controlling factors are hardly known. Naumov (1969) referred colonies with thick walled hydrothecae to a variety, *caliculata* Hincks, 1853, which he considered grew only in strong currents; but although this relation seems logical he offered no proof. In his introductory sections (p. 123) he reported that hydrothecae of this species grow larger in cool water than in warm.

DISPERSIVE STAGE. Basically a short lived medusa. But this is often retained (as a gonomedusa), when the planula is the only motile stage. The free medusa was perhaps first described by Hartlaub (1897) from Helgoland, and shortly after by Browne (1897) working independently in SW Ireland. But von Lendenfeld (1883*a, b*) had earlier described a closely similar nominal species which may prove identical, from Australia ('*Eucopella campanularia*'; see Remarks); and Agassiz (1862, as *Clytia poterium*) had still earlier described planula release from retained medusae.

The medusa, when released, is degenerate and ephemeral. It lacks organs of feeding and survives only a few days. Umbrella height *c.* 1 mm, width *c.* 0·65 mm; jelly thick, velum broad; stomach, manubrium and mouth absent; four narrow radial canals each with lobed gonad midway along; no tentacles or marginal cirri (after Russell, 1953). Apparently only one medusa at a time is produced from each blastostyle. The medusae swim actively (Hartlaub, 1897) but are probably short lived since they are presumed not to feed. They are sexually mature on release and do not develop further (Russell, 1953).

Giard (1898) has often been thought the first to have linked the medusa to its hydroid but von Lendenfeld's (1883*b*) earlier work might have been on this species (see Remarks). Giard was certainly the first to record that the medusa is not always released. He has been misquoted but his paper was quite explicit. Giard thought that time of year influenced medusa release, and so did Behner (1914) who worked on the probably conspecific Mediterranean medusa *Agastra rubra* Behner, 1914. But Stefani (1959) recorded liberation in turbulent water and retention under calmer conditions. Millard (1975; pers. comm.), however, stated that medusa release had not yet been recorded in southern African populations (see also Remarks). The factors influencing release are still unclear.

The female gonophore was recorded by several of the earlier workers but the male was not described until the work of Stefani (1956) and Hamond (1963), again excepting the much earlier and largely overlooked work of von Lendenfeld (1883*b*) on the possibly identical Australian populations.

Some authors (Russell, 1953, quoted in Rees & Thursfield, 1965; Hamond, 1963) have interpreted the retained medusae as sporosacs, but current knowledge of the life cycle confirms that they are medusoid. Following Miller (1973) they can be called gonomedusae. The often reported 'second medusa bud' near the base of the blastostyle [e.g. von Lendenfeld, 1883*b*; Giard, 1898; Hamond, 1963 (♂); Hirohito, 1969 (♀); Millard, 1975 (♀); BMNH 1915.3.6.12 (♂); also in congeneric species, Ralph, 1957] corroborates Miller's theory of descent from a gonophore producing medusae. Evidently the ancestral form produced several medusae on each blastostyle but today only one is produced at a time.

REPRODUCTIVE SEASON. Free medusae recorded May–November in British waters (Russell, 1953); June–September in NW France (Teissier, 1965); December–February & July at Naples (Lo Bianco, 1909). Some authors, from Giard (1898) onwards, have considered that medusa release occurs only towards the end of the reproductive season and that gamete release from sessile medusae occurs earlier in the year; but precise dates are unrecorded.

Teissier (1965) found reproductive structures on the hydroid stage from May to October in NW France.

DISTRIBUTION. Nearly cosmopolitan, occurring in all oceans from the intertidal to a little below Continental Shelf depths (at least in cold seas); and from the tropics to latitudes as high as 76° 40′ N (Greenland). The species is one of the most widely distributed of all hydroids. Noteworthy records from the eastern North Atlantic include: E & W Greenland (Kramp, 1929, 1943), N Norway (Mathiesen, 1928), Greece (Yamada, 1965), Black Sea (Manea, 1972; possibly also Naumov, 1960, 1969, as *Campanularia integriformis*, see Remarks), Morocco (Patriti, 1970, as *Campanularia compressa*), Ghana (Buchanan, 1957), Senegal (Leloup, 1939), Cape Verde Is (Ritchie, 1907); and the range of the species extends at least to the southernmost tip of Africa (Millard, 1975).

However, there are gaps in this wide distribution. Broch (1928) thought the species to be absent from the Kattegat, Skagerrak and Baltic, and Stechow (1927) from the Baltic alone; but Kramp (1935) and Jägerskiöld (1971) recorded it from W Sweden. Apparently there are still no records from the Baltic Sea. The species evidently did not occur in the Zuider Zee (Hummelinck, 1936) and has probably never been reliably recorded from Dutch waters (Vervoort, 1946*a*). However, it is sometimes washed ashore on the Belgian coast (Leloup, 1952).

Similarly, Irish Sea and W Scottish records are few: Bardsey I, Wales (Knight-Jones & Jones, 1956), Isle of Man (Bruce, Colman & Jones, 1963), Isle of Cumbrae, Clyde Sea (Chopin, 1894; Rankin, 1901), 10 m depth in Cregan Narrows, Loch Creran, Argyll (C. Edwards colln, pers. comm.). Chumley (1918) recorded no Clyde Sea material; and Stephens (1905) gave only a few Irish localities: Belfast, Dublin and Co Cork, the last including some of the syntypes of *Campanularia caliculata*. Possibly the only record from the west coast of Ireland is from Valencia I, Co Kerry (Browne, 1900), incidentally one of the earliest descriptions of the medusa. Hincks (1868) and Russell (1953) similarly listed no records from the western coasts of Eire and Scotland but the species is small and may have been overlooked. Broch (1918) included the NW Irish and W Scottish coasts in the North Atlantic distribution but did not cite material and may have been guessing.

Lastly, Arai & Brinckmann-Voss (1980 : 103) thought the species might not occur in British Columbia and Puget Sound.

HABITAT. World depth data range from intertidal (e.g. Hincks, 1853, British Isles) through 300 m (Broch, 1918, Davis Strait) exceptionally to 470 m (Kramp, 1929, W Greenland). The deepest records are from cold waters. The species has been recorded on a wide variety of algae, hydroids, other animals and inorganic substrates, and there is no regular association. Mathiesen (1928) recorded *O. integra* on *Laminaria* sp. to depths of *c.* 100 m off Norway. Broch (1918) regarded the species as stenohaline, a view supported by the lack of records from the Baltic Sea and Zuider Zee.

REMARKS. Several species closely related to *O. integra* were recognized by Ralph (1957), Millard (1975) and Gow & Millard (1975), and a world revision of the genus would be timely. Much discussion was provided by Arai & Brinckmann-Voss (1980).

O. integra itself is both variable and nearly cosmopolitan, and has consequently been described under many species names (*cf. Clytia hemisphaerica*, p. 73). The above synonymy includes only North Atlantic synonyms and main ones from other areas when they enter the discussion. The following notes on them are arranged in date order where possible.

Baster (1762 : pl. 2, fig, 7A, a) published some unidentified illustrations which Maitland (1876) referred to the present species. Vervoort (1946*a* : 276) regarded them as indeterminate, however, and I concur. They are discussed further under *Clytia hemisphaerica* (p. 78). Although Pallas (1766) arguably applied an earlier species name partly to Baster's illustrations, the later name *integra* is not threatened (but see the paragraph after next).

Clytia urnigera Lamouroux (1816 : 203, pl. 5, fig. 6), based on 'Australasian' material, was discussed by Couch (1844) when proposing *Campanularia laevis* Couch, a nominal species considered below. Couch noted a resemblance between the hydrothecae of *urnigera* and those of *laevis* but rightly pointed out that the narrow gonothecal aperture of *urnigera* contrasted with the wide aperture in *laevis*, and held them distinct. *C. urnigera* is here referred to *Clytia hemisphaerica* (p. 78); and *C. laevis* to *O. integra* (see below).

Clytia undulata Lamouroux, in Freycinet, 1824, was based on a fertile colony growing on 'marine plants' at Port Jackson, New South Wales. The species was regarded by Lamouroux as close to '*Clytia urnigera* Lamouroux', here referred to *C. hemisphaerica*. It was mentioned again only twice in the literature according to Bedot (1905), in 1824 and 1836, but no further taxonomic features were mentioned. *C. undulata* seems to be closer to the present species than to '*C. urnigera*' and *C. hemisphaerica*. It is mentioned here as it predates other *Orthopyxis* species and might prove conspecific with *O. integra*; but before it can be fully assessed more information is needed about the Australian populations of *Orthopyxis*.

Clytia ryckholtii Westendorp, 1843, was based on material from Ostend, Belgium. It was referred to *O. integra* by Billard (1914); and also by Leloup (1947) as '*C. Rijckholtii Slab.*'. Both Leloup's spelling and his reference to Slabber are wrong: Slabber (1769–1778) did not treat *O. integra* or anything similar. I have not located the type material; but Westendorp's illustrations show a reptant colony with long hydrothecal pedicels spirally grooved top and bottom each with an intervening smooth portion, and an even rimmed hydrotheca. They are the earliest illustrations of *O. integra* yet identified—but those of *Clytia undulata* Lamouroux, in Freycinet, 1824, which might prove conspecific, are earlier. The description of '*ryckholtii*' states the pedicels to be 3 mm long and mentions an even rimmed hydrotheca, confirming the identification. A rare and later work by Westendorp (1853) on Belgian zoophytes was illustrated by actual specimens. Had *C. ryckholtii* been included the specimens might have been types; but it was not (see note 1, p. 123), and I agree with Billard (1914) that the type material is probably lost.

Campanularia intertexta Couch, 1844, was based on a mixed type series comprising *Lafoea dumosa* (Fleming, 1820) and an unidentified campanulariid which might have been *O. integra*. *C. intertexta* is now referred to *L. dumosa* (see p. 122) but the original illustration, which included the campanulariid, was one of the earliest of *O. integra*.

Campanularia laevis Couch, 1844, type locality Polperro, Cornwall, was implicitly referred to the present species by Johnston (1847). The type material may be have been preserved for a long time in the Royal Institution of Cornwall, Truro, but if present would have been destroyed by a flood in 1953 (Curator, Roy. Inst. Cornwall, pers. comm.). Johnston (1847) mentioned material sent to him by W. W. Saunders (BMNH reg. no. 1847.9.24.65, on a herbarium sheet). The material is labelled in Johnston's hand '*Campanularia laevis!* W. Wilson Saunders, Hastings, 1840' and a label has been glued on later, also in Johnston's hand, on which is written '*Campanularia integra*'. I concur with Johnston's later identification as *O. integra*. In the absence of the original type material I designate the specimen 1847.9.24.65 neotype of *C. laevis* Couch, 1844; and extend the type locality to comprise coastal waters of the south of England. I agree also with Johnston's suggestion that the original description of *C. laevis* Couch should be referred to *O. integra*; and with the tentative but similar opinion of Bedot (1905 : 157) that the two are conspecific. Gray (1848 : 86) too referred both the species *C. laevis* and the material just mentioned to *O. integra*; but, inconsistently, on the next page gave *C. laevis* Couch full specific rank. He did this under the genus name *Capsularia* Cuvier, 1797, now regarded a junior objective synonym of *Coryne* Gaertner, in Pallas, 1774 (see Cornelius, 1975*b* : 378). Turning to a later work, it seems that Hincks' (1868 : 164) Hastings record of Saunders' material refers to the same specimen. Since Johnston (1847) did not publish the locality it seem likely Hincks deduced if from Gray (1848), who did. The junior homonym *Campanularia laevis*, Hartlaub, 1905, is discussed under *Campanularia hincksii*, which that nominal species most resembles (p. 54).

Campanularia caliculata Hincks, 1853, is the main European synonym to have been applied to the hydroid stage. When proposing the nominal taxon Hincks in fact provided the first good description of the present species. Bedot (1918) recorded that Levinsen (1893) was the first to refer *caliculata* to *integra*. Several senior authors have accepted this synonymy (e.g. Broch, 1918; Kramp, 1935; Vervoort, 1946*a*; Millard, 1975) and examination of type and non-type BMNH material supports their view. Hincks (1853) stated clearly the differences from *integra* as he saw them. They were simply: a 'double' hydrotheca and pedicel (inaccurate observation of thick walled material) and a more gradual tapering of the hydrotheca in *caliculata* than in *integra* (a variable feature). Neither character is reliable (see the above description and the discussion by Millard, 1975 : 209–210). Russell (1953) drew attention to the gonothecal contents later illustrated by Hincks (1868 : pl. 31, figs. 1a, b) as *integra*. They seemed to be sporosacs, and Russell was not entirely ready to accept the synonymy. It then seemed plausible that there were two species, one with sporosacs and the other with facultatively released medusae. The question was resolved when Millard (1975) illustrated structures similar to those shown by Hincks and described release of gametes from them. Millard had not recorded medusa release in her area (southern Africa). Still, she commented 'In partly spent gonophores the medusoid structure can sometimes be seen and is best observed by dissecting the gonophore out of the gonotheca' (op. cit., p. 209). Evidently the sessile eumedusoids (called gonomedusae by Miller, 1973) resemble sporosacs closely and their medusoid nature is not easy to see. Hence Russell's point is answered, and synonymy seems in order.

Campanularia breviscyphia Sars, 1857, was referred to *C. caliculata* Hincks, 1853, by Hincks (1868), and to the present species by Vervoort (1946*a*).

Clytia (Orthopyxis) poterium Agassiz, 1862, was a nominal species apparently based on North American material. Agassiz' description was exceptionally detailed and beautifully illustrated, but he failed to consider the several related species already described from European waters (*integra, ryckholtii, laevis, caliculata, breviscyphia*). His account suggests strongly that his material was merely *O. integra*. Hincks (1868) and Bale (1914) summarily dismissed *poterium* as conspecific; but Agassiz' account remained the most detailed of the species for many years. It was the earliest of the medusa, albeit of retained specimens. The caption to the plates included the spelling '*Clythia*', an unjustified emendation of *Clytia*.

Laomedea repens Allman, 1871, was referred to the present species by Bedot (1910) and Vervoort (1946*a*), and I concur. The originally illustrated material was said to have come from Scotland (Allman, op. cit., p. 48) and comprised only a female gonophore of *O. integra*. The nominal species was apparently never described again. Allman later applied the same specific name to another taxon, *Hypanthea repens* Allman, 1876*a*, type locality Kerguelen Island (see also p. 50).

Campanularia gracilis Allman (1876*b* : 260, pl. 12, figs 5–6), from Japan, was referred to the present species by Levinsen (1893) but this was quite unjustified. The type material (BMHN reg. no. 1877.4.12.5) is clearly distinct and not closely related to *O. integra*. Stechow (1925 : 423, fig. 6) described new material of *C. gracilis* Allman but Millard (1975 : 208) provisionally referred it to *O. integra*. However, Stechow's illustration closely resembles the type material and Millard, like Levinsen, was apparently mistaken in uniting the two taxa. Yamada (1959 : 35) evidently regarded *C. gracilis* as valid but recorded no material apart from the type.

Campanularia compressa Clarke, 1877, based on the hydroid stage, was referred to the present species by Broch (1910, 1918) and Millard (1975), although Arai & Brinckmann-Voss (1980) regarded it distinct. Other material of *O. integra* was recorded under the species name *compressa* by Stechow (1919*a*, Villefranche), Picard (1951*b*, Senegal), Picard (1958*a*, Israel) and Patriti (1970, Morocco). See also the comments on *Agastra rubra* Behner, 1914, the corresponding nominal species based on the medusa, below.

Eucopella campanularia von Lendenfeld, 1883*a*, is discussed above (p. 60).

Campanularia borealis Marktanner-Turneretscher, 1890, was based on hydroid material from Spitzbergen. No illustration was provided. Linko (1911 : 164) referred the species to *O. integra* and I concur.

Campanularia integriformis Marktanner-Turneretscher, 1890, based on hydroid material from Trieste, seems the same as *O. integra.* Naumov (1960, 1969) briefly described specimens from the Black and Adriatic Seas as *C. integriformis* but this too was probably *O. integra.* If so, Naumov's report of *O. integra* in the Black Sea predates that of Manea (1972), who had claimed the first record. Picard (1958*b*) referred *integriformis* to *caliculata* Hincks, 1853, without comment but *caliculata,* too, is now referred to *integra.*

Agastra mira Hartlaub, 1897, based on Helgoland material, has been widely regarded as the first description of the *free* medusa of *O. integra.* Browne (1897) described the medusa from SW Eire in the same year, as an unidentified leptomedusan; but a footnote in Browne's paper comments on Hartlaub's account, which had presumably already appeared. Both accounts of the medusa might be predated, however, if the closely similar Australian nominal species *Eucopella campanularia* von Lendenfeld, 1883*a*, *b*, proves conspecific.

Several authors listed by Bedot (1918, 1925) applied the combination *Agastra caliculata* to the medusa stage.

Agastra rubra Behner, 1914, a medusa from the Mediterranean, was referred to *O. integra* by Stefani (1959) and Millard (1975) among others. Its nominal hydroid, *Campanularia compressa* Clarke, 1877 (see above), was referred to *O. integra* by Broch (1910, 1918); and both stages were so treated by Millard (1975). Kramp (1961), however, considering the medusa stage alone, held *A. rubra* distinct on the shape of the gonads. Further work seems necessary to resolve these different views, but the majority opinion is that *A. rubra* is invalid.

Finally, the type material of *Orthopyxis asymmetrica* Stechow, 1919*a*, from Marseille, was examimed and found merely to be *O. integra.* Philbert (1935*a*) described growth forms under this name.

Genus ***RHIZOCAULUS*** Stechow, 1919*b*

Sertularia Linnaeus, 1758 : 811 (part).
Campanularia Lamarck, 1816 : 112 (part); Hincks, 1868 : 160 (part).
Rhizocaulus Stechow, 1919*b* : 852; Stechow, 1919*c* : 16.
Verticillina Naumov, 1960 : 9, 115, 122, 269; Naumov, 1969 : 6, 115, 123, 291.

TYPE SPECIES. *Sertularia verticillata* Linnaeus, 1758; by original designation.

DIAGNOSIS. Campanulariidae forming erect, polysiphonic colonies; hydrothecae in whorls; no true hydrothecal diaphragm; sub-hydrothecal spherule present; no medusa stage.

REMARKS. Nutting (1915 : 28) designated *Sertularia verticillata* Linnaeus, 1758, type species of the genus *Campanularia* Lamarck, 1816, but for the reasons given under that genus (p. 51) I have applied to the International Commission on Zoological Nomenclature for that designation to be set aside (Cornelius, 1981).

Rees & Thursfield (1965) opposed the erection of a distinct genus to accommodate *verticillata* on the grounds that in *Lafoea* Lamouroux, 1821, family Lafoeidae, there are both stolonal and erect colonies; but colony habit does not have the same taxonomic value in all families, and the separation is upheld here.

Stechow (1919*b*) listed several nominal species in the genus but they may prove conspecific with *R. verticillatus.*

Rhizocaulus verticillatus (Linnaeus, 1758)
(Fig. 7)

Corallina ramosa, ramis singulis equisitiformibus in summis capillamentis contortis et verticillatim dispositis . . . Ellis, 1755 : 23–24, pl. 13, figs A, a.
Sertularia verticillata Linnaeus, 1758 : 811.
Campanularia verticillata: Lamarck, 1816 : 113; Hincks, 1868 : 167–168, pl. 32, fig. 1, 1a; Goette, 1907 : 179–189, pl. 14, figs 294–304, pl. 15, figs 305–306; Linko, 1911 : 188–200, fig. 35 (syn. *Clytia olivacea* Lamouroux, 1821).
Clytia olivacea Lamouroux, 1821 : 13, pl. 67, figs 1–2.
Campanularia verticellata Couch, 1842 : 49 (lapsus).

Campanulata verticillata: Agassiz, 1862 : 354, footnote (unjustified emendation of *Campanularia*).
Rhizocaulus verticillatus: Stechow, 1919*b* : 852: Stechow, 1919*c* : 16; Stechow, 1923*a* : 105–106.
Verticillina verticillata: Naumov, 1960 : 269–270, fig. 159; Naumov, 1969 : fig. 159.

TYPE MATERIAL AND LOCALITY. Linnaeus (1758) provided only a diagnosis of this species, implying that he did not see material (*cf.* Cornelius, 1979 : 309). Indeed, there is none in the Linnaeus collection held by the Linnean Society of London (Savage, 1945). Linnaeus (1758) cited only the illustration of Ellis (1755 : pl. 13, fig. A, but not fig. a), and the colony Ellis illustrated can be regarded as holotype. It was collected from the coast of Cumberland, NW England, to which the type locality can be restricted. The specimen is almost certainly now lost (Cornelius, 1975*a* : 267, footnote).

MATERIAL EXAMINED. BMNH collections, about 40 specimens. Some northerly material deserves mention: Barents Sea, 74° 8′ 50″ N, 30° 31′ 28″ E, 375 m, 1882, ex D'Arcy Thompson collection; 1956.10.23.180.

DESCRIPTION. Colony large, erect, occasionally and irregularly branched; stems polysiphonic with pedicels roughly in whorls, recalling the terrestrial horse-tail plants (*Equisetum* L.). Component perisarc tubes straight, parallel, each bearing straight, smooth or spirally grooved hydrothecal pedicels (sometimes annulated, e.g. Fig. 7) at approximately regular intervals. Hydrotheca bell shaped, sub-hydrothecal spherule present; rim with *c.* 12 blunt cusps. Gonotheca ?♂ = ♀, flask shaped, with neck of varied length; on short pedicel.

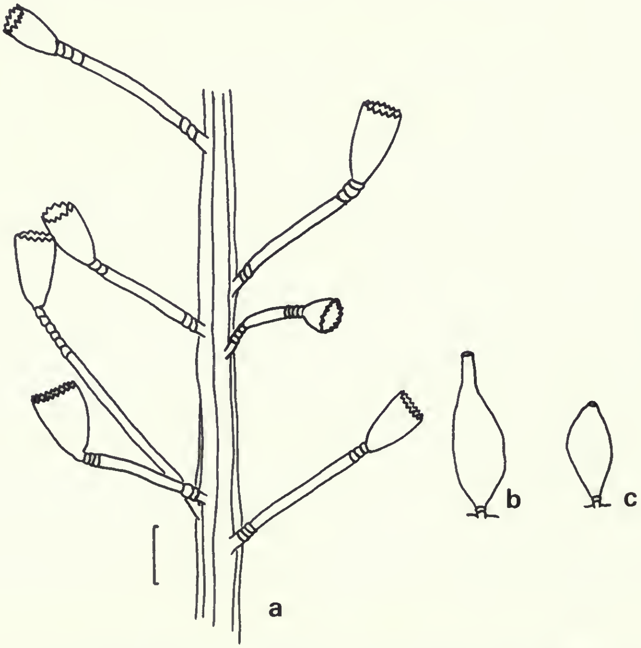


Fig. 7 *Rhizocaulus verticillatus.* (a) part of colony, Isle of Man, 25 March 1894; 1948.10.1.21. (b) gonotheca with long neck, 30–40 m depth, nr Bergen, 15 August 1962; 1962.11.7.8. (c) gonotheca with short neck, 45 m depth, W Scotland; 1888.4.2.39. Scale (a–c) 500 μm.

DISPERSIVE STAGE. Planulae, probably developing within the gonotheca. Early gonophore development was described by Goette (1907). No medusa.

REPRODUCTIVE SEASON. Fertile material recorded May, 1934, off NE England (H. O. Bull, in Evans, 1978); July, NW France (Teissier, 1965); 15 August, 1962, nr Bergen, Norway (BMNH reg. no. 1962.11.7.8).

DISTRIBUTION. Widespread in sublittoral and coastal waters from Tromso, Norway (Mathiesen, 1928) and Danmarks Havn, Greenland (Kramp, 1943) at least to Roscoff, NW France (Teissier, 1965). The species is well known from offshore areas of Britain, the Netherlands, Belgium, Denmark and Sweden. See also Material examined.

The status of *R. verticillatus* along the W coast of France and the Bay of Biscay is unclear. Vervoort (1946*a*) and Naumov (1969) recorded it but the species was not listed in several local faunal surveys (Billard, 1927; Nobre, 1931; Da Cunha, 1944, 1950; Fey, 1969) and there is no BMNH material from south of the English Channel. Picard (1958*b*) did not record the species from the Mediterranean Sea; but Manea (1972) provided an acceptable record from the Black Sea, possibly the farthest south the species has been found on European coasts.

HABITAT. Naumov (1969) gave a usual depth range of 50–200 m, with extremes of 15 m and 680 m. Mathiesen (1928) gave a range of 20 m to 600 m in S Norway.

Hamond (1957) associated the species with 'sandy grounds' off the Norfolk coast, but Teissier (1965) recorded it on algae in NW France. Hincks (1868) and Leloup (1952) found the species on pebbles and shells. *R. verticillatus* seems to occur typically on occasional solid substrates in otherwise sandy areas.

REMARKS. There seems no need for revision of this distinctive species. Rees & Thursfield (1965) drew attention to the superficial similarities between it and *Campanularia volubilis* (but see p. 57).

The development and structure of the compound stem of *R. verticillatus* was studied by Schach (1935).

The combination *Campanularia verticillata* var. *grandis* Hickson & Gravely, 1907, related to an antarctic species now known as *Stegella grandis* (Hickson and Gravely) and assigned to the Campanulinidae (e.g. Totton, 1930; Stepanyants, 1979). The similarity in colony form is striking but *S. grandis* lacks a sub-hydrothecal spherule and the hydrothecal rim is quite different.

Subfamily **CLYTIINAE** nom. nov.

Phialidae Haeckel, 1879 : 163 (part).
Phialinae: Mayer, 1910 : 232 (part).
Campanularinae: Russell, 1953 : 284.

DIAGNOSIS. Campanulariidae with a usually reptant, branched but not anastomosing stolon; with true hydrothecal diaphragm; usually without subhydrothecal spherule (but present in *Clytia hummelincki*); medusa present in some genera, a typical leptomedusa with prominent velum.

SCOPE. The genera *Clytia* Lamouroux, 1812; *Gastroblasta* Keller, 1883; and *Tulpa* Stechow, 1921*a*. *Gastroblasta* and *Tulpa* have not been recorded in the eastern North Atlantic and are discussed only under Remarks, but *Clytia* is treated below.

TYPE GENUS. *Clytia* Lamouroux, 1812.

REMARKS. Previous subfamily names applied in part to this group (Phialidae Haeckel, 1879; Phialinae Mayer, 1910) have been derived from *Phialium* Haeckel, 1897, the name of a genus now referred to the Lovenellidae (Mayer, 1910; Kramp, 1961). *Phialium* can be taken as type genus of the nominal subfamily Phialiinae; and there seems no available name for the present group.

There has no doubt been confusion between *Phialium* Haeckel and *Phialidium* Leuckart, 1856. *Phialidium* is today referred to *Clytia* Lamouroux, 1812, and basing a new subfamily name on *Phialidium* might be confusing. Haeckel (1879 : 186) indicated that he understood the relation between *Phialidium* and *Clytia* by including *Clytia johnstoni* sensu Böhm in the synonymy of *P. variable.* This relationship had only just been understood (p. 76) and Haeckel might have been reticent to consider all the nomenclatural implications.

The subfamily name Clytiinae is to be considered a nom. nov. applied to the present subfamily as restricted by Russell (1953) under the preoccupied name Campanulariinae. It should not be confused with family group names derived from *Clytus*, a coleopteran genus name. These are spelt Clytinae, Clytini and so on (C. R. Smith, pers. comm.), being derived from the root Clyt. The root from which Clytiinae is derived is Clyti.

The genus *Gastroblasta* Keller, 1883 : 622, is now restricted to a single, distinctive medusa species based on Red Sea material (Kramp, 1961). The name was once applied to species now referred to one or other of the *Clytia* species treated below (discussion on p. 72).

The genus *Tulpa* Stechow, 1921*a* : 254, was proposed to embrace three species none of which has been recorded from the eastern North Atlantic. The type species is *Campanularia tulipifera* Allman, 1888, by original designation (= *C. tulpifera* lapsus auct.). The genus was accepted by Totton (1930) who described another species. *Tulpa* was reviewed by Ralph (1957) and redefined by Stepanyants (1979); and discussed also by Vervoort (1972) and Gravier-Bonnet (1979) who gave systematic notes.

Genus *CLYTIA* Lamouroux, 1812

Medusa: Linnaeus, 1767 : 1096 (part).
Sertularia Ellis & Solander, 1786 : 51 (part).
Oceania Péron & Lesueur, 1810*a* : 343 (part).
Clytia Lamouroux, 1812 : 184.
Campanularia auct., part (see Remarks under *Clytia hemisphaerica*, p. 77).
Thaumantias Eschscholtz, 1829 : 102; Forbes, 1848 : 52 (part).
Silicularia Meyen, 1834 : 206 (part; see p. 50).
Eucope Gegenbaur, 1856 : 241 (part).
Phialidium Leuckart, 1856 : 18; Kramp, 1961 : 164.
Epenthesis McCrady, 1857 : 191; Haeckel, 1879 : 182.
Clytia (Trochopyxis) Agassiz, 1862 : 304.
Clytia (Platypyxis) Agassiz, 1862 : 306.
Clytea Wright, 1862 : 308 (lapsus pro *Clytia).*
Clythia van Beneden, 1866 : 166 (lapsus pro *Clytia*).
Gastroblasta auct., part (*non* Keller, 1883, s. str.).
Pseudoclytia Mayer, 1900 : 53.
Multioralis Mayer, 1900 : 54.
non *Clythia* Agassiz, 1862 : pl. 28 (lapsus pro *Clytia,* but referred to *Orthopyxis*, p. 57).

TYPE SPECIES. There were three species originally included in the genus, listed thus: '*Sertularia volubilis* Ellis, *S. syringa* Ellis, *S. verticillata* Ellis'. The descriptions cited are presumably those of Ellis & Solander (1786), in which book binominals were employed, and not those of Ellis (1755) which lacked them. The point is important since '*S. volubilis* sens. Lamouroux, 1812' was subsequently designated type species (see next paragraph). Confusion was caused when Lamouroux himself (in Lamouroux, Bory de Saint-Vincent & Deslongchamps, 1824 : 202) later applied the name *S. volubilis* to another species, citing therein the Ellis, 1755, illustration which in fact shows the species here called *Campanularia volubilis* (p. 55). Lamouroux' (1812) earlier citation, then, refers to *Sertularia volubilis* Ellis & Solander, 1786 [= the nominal hydroid species *Clytia johnstoni* (Alder, 1856*a*), usually regarded the same as the medusa *Clytia hemisphaerica* Linnaeus, 1767; see p. 77]; and the later citation (Lamouroux *et al.*, 1824), employing the same combination, refers to *Campanularia volubilis* (Linnaeus, 1758) (see p. 77 for further discussion).

The type species of *Clytia* might appear to be *Sertularia volubilis* Ellis & Solander, 1786 (non Linnaeus, 1758, see above), as designated by Mayer, 1910 : 262; but as just explained the combination is a junior homonym. This would be unimportant to current nomenclature if the hydroid *Sertularia volubilis* Ellis & Solander, 1786, were definitely known to be the same species as *Medusa hemisphaerica* Linnaeus, 1767. A relation is usually assumed (see notes under *Clytia hemisphaerica*, p. 79), and Linnaeus indicated Gronovius' (1760 : pl. 4, fig. 7) illustrated specimen, collected from Belgian waters (the type locality of *hemisphaerica*). The illustration shows a strongly convex exumbrella surface, suggesting *C. hemisphaerica* sens. auct. (e.g. p. 73); but the lingering doubts over the identity of the hydroid *C. gracilis* (Sars, 1850; see p. 78) make the relation of the two nominal species uncertain. Therefore, it is useful to establish a soundly based name for the type species of the genus *Clytia*. The earliest available name which can be unequivocally linked with *S. volubilis* sens. Ellis & Solander, 1786, is *Campanularia johnstoni* Alder, 1856*a*. Hence the correct name for the type species of *Clytia* is *C. johnstoni*. The often quoted synonymy with *C. hemisphaerica*, repeated below, is subjective. See also Cornelius (1981), and page 78 concerning the very similar '*Laomedea gracilis*' Sars, 1850.

DIAGNOSIS. Colonial Campanulariidae with free medusa stage; hydroid generation forming umbranched stoloniferous or branched upright colonies; hydrotheca with true diaphragm, rim sinuous to deeply indented with round to sharp clefts and cusps; diaphragm transverse; no sub-hydrothecal spherule; medusa hemisphaerical to flat, with hollow marginal tentacles, velum well developed; manubrium short; 4–8 marginal tentacles on release (in species so far studied), many tentacles in adult.

REMARKS. A summary of the species of *Clytia* in which the life cycles have been worked out was given by West & Renshaw (1970); and Roosen-Runge (1970) and Arai & Brinckmann-Voss (1980) gave detailed appraisals of several North American species.

Early generic names applied to the type species were broad in concept (*Sertularia volubilis = Medusa hemisphaerica = Campanularia johnstoni*) and the diagnosis of them by successive workers often overlapped. Hence it is not unexpected that species now included in *Clytia* s. str. should at one time or another have been included in one or more other genera. There is little value in discussing past uses of generic names such as *Medusa, Sertularia, Oceania* and *Campanularia* for species now referred to *Clytia*.

The name *Thaumantias* Eschscholtz, 1829, was also once widely used. It is a junior subjective synonym of *Clytia*, since Forbes (1848 : 41) nominated *Medusa hemisphaerica* Linnaeus, 1767, its type species. This medusa is, of course, widely held to come from the hydroid which is type species of *Clytia*; but the link is neverthless subjective and is likely to remain so as the original description of the medusa was brief.

The genus *Silicularia* Meyen, 1834, is discussed on page 50.

Availability of the generic name *Eucope* Gegenbaur, 1856, was discussed by Haeckel (1879), Mayer (1910), Rees (1939) and Russell (1953) among others. The four originally included species were referred to *Obelia* and *Clytia* (or *Phialidium*) by Mayer and subsequent authors; but so far as I can determine no type species has been designated. Russell (1953) referred three of the originally included species (*E. thaumantoides, E. campanulata & E. affinis*) to *Clytia hemisphaerica* (as *Phialidium*); and the remaining one (*E. polystyla*) is *Obelia* (e.g. following Cornelius, 1975*a*). I designate *E. affinis* Gegenbaur, 1856, type species of *Eucope*, which falls in the subjective synonymy of *Clytia* (see also Bedot, 1910 : 414 and Hincks, 1868 : 143).

The genus *Phialidium* Leuckart, 1856, was based on a single species, *P. viridicans* Leuckart (1856 : 18–19, pl. II, figs 12, 14) which is therefore type by monotypy. Mayer (1910) confirmed its type status, and Kramp's (1961) designation of '*P. hemisphaericum* L.' is incorrect. Russell (1953) drew attention to the close similarity between *P. viridicans* and *Clytia hemisphaerica,* including them in the same species synonymy. Thus the case for regarding *Clytia* and *Phialidium* congeneric is strong and *Phialidium,* being the later name, need no longer be used.

The genus *Epenthesis* McCrady, 1857, was referred to *Clytia* by Mayer (1910 : 261) and Nutting (1915 : 1) among others. The name is clearly a junior synonym of *Clytia*.

The subgenus *Platypyxis* Agassiz, 1962, was referred to *Clytia* by Bedot (1910), and I concur (see Remarks under *C. hemisphaerica*).

The genus *Gastroblasta* Keller, 1883, now includes just one species, from the Red Sea. All other uses of the generic name have related to abnormal medusae of *Clytia* species (Kramp, 1961; also Mayer, 1910, Kramp, 1957, 1965).

The genera *Multioralis* Mayer, 1900, and *Pseudoclytia* Mayer, 1900, were referred by Kramp (1957, 1961) to *Phialidium* Leuckart, 1856, and hence fall into *Clytia.*

Luminescence has long been known in the genus (e.g. Darwin, 1860 : ch. 2, hydroid stage; other references in Forbes, 1848, medusa stage). Light emission was probably first recorded in *Clytia* by Macartney (1810). In October, 1804, he demonstrated to an invited audience at Herne Bay, Kent, that flashing in the medusa of *C. hemisphaerica* (which he called *Medusa lucida*) was induced by raised temperature, electric shock and alcohol. His published illustration of the medusa is among the earliest of the genus.

Clytia discoida (Mayer, 1900)
(Fig. 8)

Oceania discoida Mayer, 1900 : 51, pl. 20, figs 53–55.
Phialidium discoidum Mayer, 1910 : 272, pl. 33, figs 9–11; Kramp, 1959 : 148, fig. 187; Kramp, 1961 : 165–166; Schmidt & Benovič, 1977 : 637.

TYPE LOCALITY. Tortugas, Florida; in plankton.

MATERIAL EXAMINED. None.

DESCRIPTION (after Mayer, 1910; Kramp, 1959; Schmidt & Benovič, 1977). Adult medusa 'quite flat' (Mayer), about 4 mm diameter; 16 short marginal tentacles with large basal bulbs; usually 3 statocysts between tentacle bases; velum well developed; 4 straight radial canals; gonads along almost whole length, eggs in ♀ unusually large and prominent; manubrium 'urn-shaped' (Mayer) with 4 recurved lips. Hydroid stage not recorded.

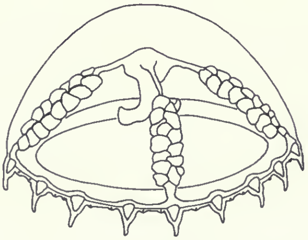


Fig. 8 *Clytia discoida.* Adult medusa. Diameter *c.* 4 mm. Redrawn after Mayer (1910 : pl. 33, fig. 10).

DISPERSIVE STAGE. The species is known from the medusa alone. See also notes under Dispersive stage of *C. linearis.*

REPRODUCTIVE SEASON. Summer; June–August (Mayer, 1900; Schmidt & Benovič, 1977).

DISTRIBUTION. Recorded from: Florida, Mexico, Brazil and W. Indies (references in Kramp, 1961); southern Adriatic Trough (once only, Schmidt & Benovič, 1977). Several records from the Pacific Ocean were discredited by Kramp (1961).

HABITAT. Coastal plankton.

REMARKS. The species is distinguished by its small size at maturity and by the extension of the gonads along almost the entire length of the radial canals. Kramp (1959, 1961) seems mistaken in stating the umbrella to be 'almost hemispherical'. Others have reported it nearly flat in the adult (Mayer, 1900, 1910; Schmidt & Benovič, 1977). However, younger stages are reportedly less flat (Mayer), but Schmidt & Benovič reported a young specimen only

1·5 mm in diameter which was already 'more flat than hemispherical'. The adult diameter is 4 mm.

The species is known in the NE Atlantic from a single Adriatic specimen (Schmidt & Benovič, 1977). Kramp (1961) provided a literature synopsis.

Clytia hemisphaerica (Linnaeus, 1767)
(Fig. 9)

Medusa hemisphaerica Linnaeus, 1767 : 1098; Müller, 1776 : 233.
Sertularia uniflora: Ellis, 1768 : 434, pl. 19, fig. 9.
Sertularia volubilis: Ellis & Solander, 1786 : 51, pl. 4, figs E, e, F, f (non *S. volubilis* Linnaeus, 1758; see p. 76 and Remarks).
Oceania flavidula Péron & Lesueur, 1810*a* : 345; Péron & Lesueur, ?1810*b* : 33.
Oceania hemisphaerica: Péron & Lesueur, 1810*a* : 347; Péron & Lesueur, 1810*b* : 35.
Clytia urnigera Lamouroux, 1816 : 203, pl. 5, fig. 6 (see Remarks under *Orthopyxis integra*).
Thaumantias inconspicua Forbes, 1848 : 52, pl. 8, fig. 3 a–d; Ritchie, 1911 : 31.
?*Laomedea gracilis* Sars, 1850 : 138; Sars, 1857 : 160, pl. 2, figs 1–3, 5 (but not fig. 4, = *Gonothyraea loveni*; see Stechow, 1923*a* : 111); (*non* Dana, 1846 = *Obelia dichotoma*).
Campanularia volubilis: (sens. Ellis & Solander) Hincks, 1852 : 84–85, pl. 3, fig. 5 (see Dispersive stage and Remarks).
Campanularia sp. Gegenbaur, 1854 : 154, 189, pl. 1, figs 8, 8a, 9.
Campanularia johnstoni Alder, 1856*a* : 359–360, pl. 8, fig. 8 (nom. nov. pro *Sertularia volubilis* Ellis & Solander, 1786).
?*Phialidium viridicans* Leuckart, 1856 : 18–19, pl. 1, figs 12, 14 (see pp. 71, 86).
?*Clytia noliformis* McCrady, 1857 : 194–195, pl. 11, fig 4; Fraser, 1944 : 144–145, pl. 26, fig 117 (syn. *C. simplex* Congdon).
Campanularia gegenbauri Sars, 1857 : 48–49.
Campanularia volubiliformis Sars, 1857 : 156 (nom. nov. pro *Campanularia* sp. Gegenbaur, 1854).
Campanularia raridentata Alder, in Hincks, 1861*b* : 292; Hincks, 1868 : 176–177, fig. 2.
Clytia (Trochopyxis) bicophora Agassiz, 1862 : 304–305, pl. 29, figs 6–9.
?*Clytia (Platypyxis) cylindrica* Agassiz, 1862 : 306–307, 354, text-figs 41–44, pl. 27, figs 8–9.
Clytea vicophora Wright, 1862 : 308 (unjustified emendation of *Clytia bicophora*).
Campanularia ?gigantea Hincks, 1866 : 297; Hincks, 1868 : 174–175, pl. 35, fig. 1; Jaderholm, 1909 : 19, 33, 69, pl. 7, figs 1–3.
Clytia johnstoni: Hincks, 1868 : 143–146, pl. 24, figs 1, 1a (syn. *Sertularia volubilis* Ellis & Solander; *Eucope campanulata* Gegenbaur; *E. thaumantoides* Gegenbaur; *E. affinis* Gegenbaur; *Campanularia gegenbauri* Sars; *Clytia bicophora* Agassiz; see Remarks); Böhm, 1878 : 167–171, pl. 2, figs 1–9 (syn. *Platypyxis cylindrica* Agassiz; *Eucope picta* Keferstein & Ehlers, 1861; *E. exigua* Keferstein & Ehlers, 1861; *E. variabilis* Claus; *E. gemmifera* Keferstein; *Thaumantias dubia* Kölliker; *T. thompsoni* Forbes; *T. convexa* Forbes); Billard, 1928 : 456–457 (syn. *C. raridentata* Hincks); Russell, 1953 : 293, fig. 179; Ralph, 1957 : 823–824, figs 1h–u, 3a–f (syn. *C. compressa* Totton, 1930).
Clytia volubilis: Du Plessis, 1871 : 167–170, pl. 2; Hargitt, 1909 : 373–374.
Clytia laevis Weismann, 1883 : 158–159 (see Remarks under *Campanularia volubilis*, p. 57).
Clytia flavidula: Metschnikoff, 1886*a* : 241–243, 257, 260, pl. 22, figs 9–10, 15.
Campanularia? serrulata Bale, 1888 : 757, pl. 12, fig. 4.
Campanularia raridentata var. Marktanner-Turneretscher, 1890 : 205, pl. 3, figs 3a–b.
Thaumantias hemisphaerica: Browne, 1896 : 480–482 (syn. *Medusa cymbaloidea* Slabber, 1775; *M. campanella* Shaw & Nodder, 1795; *M. lucida* Macartney, 1810; *Thaumantias lucida:* Lesson, 1843; *Epenthesis cymbaloidea* Haeckel, 1879).
Campanularia inconspicua: Calkins, 1899 : 349.
?*Campanularia attenuata* Calkins, 1899 : 350, pl. 2, figs 9, 9a–c, pl. 6, fig. 9d.
?*Campanularia edwardsi* Nutting, 1901*b* : 346, fig. 28.
?*Campanularia pelagica* Van Breemen, 1905 : 205–209, fig. 18.
Clytia simplex Congdon, 1907 : 471–472, figs 14–15.
Clytia obeliformis Stechow, 1914 : 128–129, fig. 6.
?*Clytia pelagica:* Billard, 1917 : 539–542, fig. 1.
?*Clytia serrulata:* Stechow, 1919*a* : 46–47, fig. M.

Campanularia acuta Stechow, 1919*a* : 54 (nom. nov. pro *C. raridentata* var. Marktanner-Turneretscher).

Campanularia ?attenuata Stechow, 1919*a* : 61–62, fig. S (non Calkins, 1899).

Campanularia brachycaulis Stechow, 1919*a* : 62–63, fig. T.

Orthopyxis volubiliformis: Stechow, 1919*a* : 70.

Campanularia villafrancensis Stechow, 1919*a* : 157 (nom. nov. pro *C. attenuata* Stechow, 1919*a* (sic) : 61, preoccupied).

Clytia uniflora: Stechow, 1923*a* : 111 (non *Sertularia uniflora* Pallas).

Thaumantias raridentata: Stechow, 1923*a* : 107–108, fig. 17.

Clytia villafrancensis: Stechow, 1923*a* : 109–110.

Clytia compressa Totton, 1930 : 146–148, text-fig. 6.

?*Phialidium bicophorum:* Thiel, 1935 : 172; Kramp, 1959 : 149; Kramp, 1961 : 164–165.

?*Laomedea pelagica:* Vervoort, 1946*a* : 285–288; Vervoort, 1959 : 313–315, fig. 55b–c; Vervoort, 1968 : 15–17, fig. 5; Vervoort, 1972 : 91–92, fig. 26c.

Laomedea gigantea: Leloup, 1952 : 161, fig. 93.

Phialidium hemisphaericum: Billard, 1928 : 457 (syn. *Thaumantias inconspicua* Forbes); Kramp, 1919 : figs 16–17 (syn. *P. temporarium* Browne, 1896; *Thaumantias buskiana* Gosse, 1853); Russell, 1953 : 285–294, pl. 16, fig. 1, pl. 17, fig. 6, text-figs 172–179 (syn. *Thaumantias pileata* Forbes, 1841; *T. sarnica* Forbes, 1841; *T. thompsoni* Forbes, 1841; *T. punctata* Forbes, 1841; *T. lineata* Forbes, 1848; *T. hemisphaerica*: Forbes, 1848; *T. inconspicua* Forbes, 1848, Hincks, 1868; *T. buskiana* Gosse, 1853; *Eucope affinis* Gegenbaur, 1856; *E. campanulata* Gegenbaur, 1856; *E. thaumantias* Gegenbaur, 1856; *Phialidium viridicans* Leuckart, 1856; ?*T. typica* Green, 1857; *Clytia johnstoni:* Hincks, 1868; *T. leucostyla* Spagnolini, 1876; *Campanulina acuminata* Böhm, 1878; *Epenthesis cymbaloidea* Haeckel, 1879; *P. variabile* Claus, 1881; *Clytia flavidula* Metschnikoff, 1886; *C. viridicans* Metschnikoff, 1886; *P. buskianum* Browne, 1896; *P. temporarium* Browne, 1896; *T. forbesi* Johansen & Levinsen, 1903; *Clytia volubilis:* Sverdrup, 1921; for these references see Russell, 1953); Kramp, 1955 : 256–257 (syn. *P. variabile* Haeckel, 1879; ?*Oceania languida* Agassiz, 1862).

Clytia hemisphaerica: Rees & Thursfield, 1965 : 95–96; Millard, 1966 : 478–480, fig. 14a–f; Vervoort, 1968 : 16–17; Calder, 1975 : 300–302, fig. 4a–b; Millard, 1975 : 217–218, fig. 72a–d.

Clytia gigantea: Rees & Thursfield, 1965 : 96–97.

Thaumantias raridentata: Teissier, 1965 : 17.

?*Laomedea (Clytia) pelagica* Garcia Corrales *et al.*, 1978 : 28–29, fig. 11.

?*Campanularia gracilis:* (sensu Sars, 1850) Stepanyants, 1979 : 32, pl. 5, fig. 3 (syn. *Clytia serrulata:* Vanhöffen, 1910).

?*Clytia sarsi* Present paper, p. 78 (nom. nov. pro *Laomedea gracilis* Sars, 1850, preocc; see p. 78).

For further synonmy see Bedot (1901–1925), Russell (1953) and Kramp (1961). Kramp cited just the following combinations from the World literature not included in Russell's British list: *Gastroblasta raffaelei, Clythia johnstoni*, ?*Phialidium languidum* (provisionally retained distinct by Kramp), *Pseudoclytia pentata* f. *hexaradiata.* See also *Clytia* incertae sedis (p. 91).

NOMENCLATURE. Millard (1966) has shown that the apparent use of the species name *hemisphaerica* by Gronovius (1760) was not strictly binominal. Neither also was that by Houttuyn (1770 : 423), cited by Bedot (1901 : 486) as *Medusa hemisphaerica,* despite the implication of Bedot's entry. Bedot dated Houttuyn's work as 1761–1773; but the volume in which the *hemisphaerica* reference appeared was published in 1770, three years after Linnaeus' (1767) introduction of the genuine binominal *Medusa hemisphaerica.* Linnaeus cited Gronovius' illustration as indication.

The combination *Clytia hemisphaerica* results from the subjective linking of hydroid and medusa, and was probably first used by Rees & Thursfield (1965). The next year, Millard (1966) too discussed the combination.

Many authors have placed *hemisphaerica* in the 'medusa' genus *Phialidium* Leuckart, 1856; but *Clytia* Lamouroux, 1812, is older and now the life cycle is known should be used instead. The reason why *Phialidium* need not be used for any species is given above (p. 71).

Browne (1896) incorrectly ascribed the combination *Medusa hemisphaerica* to Müller, whose work Browne dated as 1766. The correct date of Müller's work was 1776, and Linnaeus (1767) has clear priority.

TYPE LOCALITY AND MATERIAL. The type material of *C. hemisphaerica* Linnaeus, 1767, was the medusa described and illustrated by Gronovius (1760 : 38, pl. 4, fig. 7). I have not tried to find it. Linnaeus gave the type locality as 'Belgian seas', from whence Gronovius' material came.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. I have examined the type series of the hydroids *Campanularia johnstoni* Alder, 1856*a*, and *C. raridentata* Alder, in Hincks 1861*b*, and consider them to be *C. hemisphaerica* (see Cornelius & Garfath, 1980; see also Remarks). The holotype colonies of the hydroids *C. ?gigantea* Hincks, 1866 (BMNH reg. no. 1899.5.1.106, Lamlash, Arran, W Scotland) and *Clytia obeliformis* Stechow, 1914 (Munich Zoological Museum, fertile colony on microslide, Bergen) are also *Clytia hemisphaerica*.

OTHER MATERIAL EXAMINED. This species is well represented in the BMNH collections. The following material, from other Museums, deserves mention: 53° 01′ N, 4° 22′ E, numerous colonies in spirit, coll. Lightship 'Texel', 1961, *cf.* '*Laomedea pelagica*' (sensu Van Breemen), det. W. Vervoort; Rijksmuseum van Natuurlijke Historie, Leiden. 10° 40′ N,

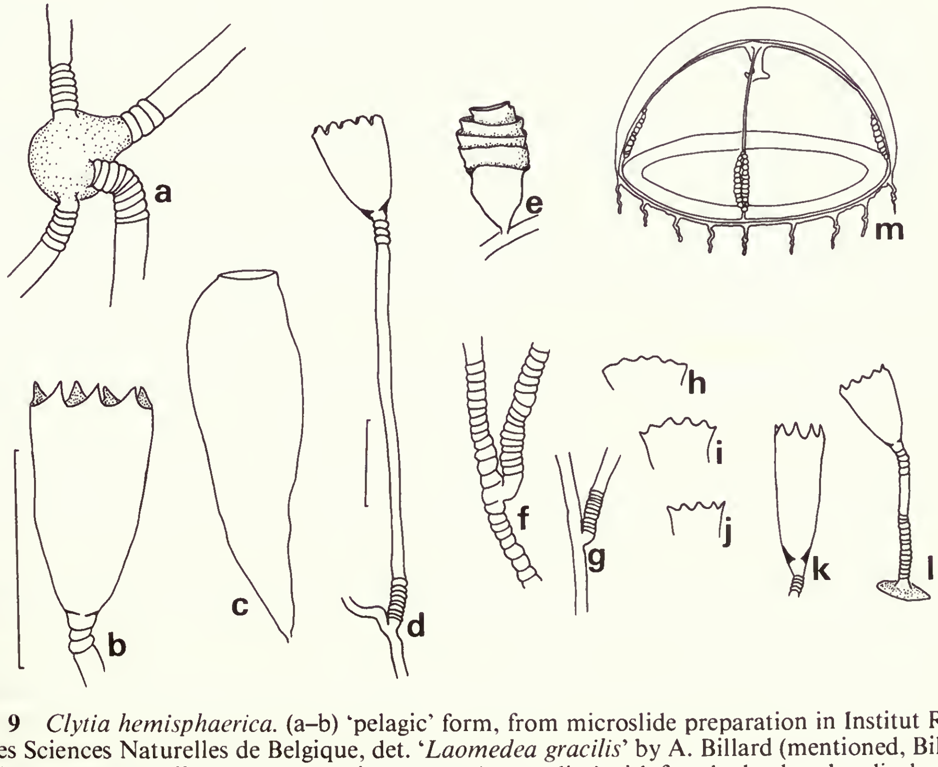


Fig. 9 *Clytia hemisphaerica.* (a–b) 'pelagic' form, from microslide preparation in Institut Royal des Sciences Naturelles de Belgique, det. '*Laomedea gracilis*' by A. Billard (mentioned, Billard, 1917; 'probably off Ostend'). (a) 'primary attachment disc' with four hydrothecal pedicels. Note absence of stolon. (b) hydrotheca. (c) 'pelagic form', gonotheca, 53° 01′ N, 4° 22′ E, det. '*Clytia pelagica*' by W. Vervoort; colln Rijksmuseum van Natuurlijke Historie, Leiden. (d–e) 'benthic form'; (d) hydrotheca and (e) gonotheca, S England; 1934.8.17.19. (f) 'benthic form', base of pedicel branch from extremely sheltered locality, Caol Scotnish, Loch Sween, Argyll, W Scotland, 1 m, 30 May 1962; 1962.6.19.21. (g) 'benthic form', base of pedicel branch, nr Bergen, 40–90 m, 9 April 1962; 1962.10.7.19. (h–j) three hydrothecal rims from same colony, Scotland; 1964.8.7.72. (k) hydrotheca, W Sweden, 20–30 m; 1962.11.8.10. (l) primary hydrotheca and attachment disc, reared from medusa ('*Phialidium hemisphaericum*' sens. Russell, 1953) by W. J. Rees, 2–17 March 1936; 1969.12.2.2. (m) medusa, Naples, redrawn after Mayer (1910 : text-fig. 144). Scales: (a–c, d–l) 500 μm; (m) unknown. See also Fig. 14(a).

6° 44′ W, 65 m, many colonies in spirit, coll. 'Atlantide' expedition, sta. 151, 16 Apr 1946, *cf.* '*L. pelagica*', det. W. Vervoort; RMNH, Leiden. Sète, S France, infertile material on three microslides, det. *Clytia serrulata* by Stechow, 1919*a* : 46; Munich Zoological Museum.

DESCRIPTION OF HYDROID STAGE. Among the most variable of all Atlantic hydroids. Detached colonies can continue growing in the plankton and form one extreme of variation, while benthic colonies are more typical of the species and form the other.

1. *Benthic colonies.* Colony comprising a creeping stolon from which short to long hydrothecal pedicels arise at irregular intervals. Hydrotheca thin walled, campanulate, length : breadth ratio 1–3, rim with 7–16 pointed to rounded or (?rarely) flat topped cusps, embayments typically pointed but sometimes rounded; hydrotheca usually round in cross-section but sometimes (Vervoort, 1968) sinuous near the top. Hydranth with the wide range of 20–30 tentacles (Hincks, 1868; *cf. Obelia geniculata*, p. 120). Pedicel straight, erect; annulated, usually with smooth central region and 2–10 annuli each end, rarely annulated throughout; sometimes branched, each branch having characteristic upward-curved basal region (similar to that in *C. paulensis*), branches often parallel with main pedicel; branch annulated basally and distally, central portion smooth. Gonotheca ♂ = ♀, broad, tubular, sometimes asymmetric, walls smooth to deeply concertinered, often with slight sub-terminal constriction; tapered below; aperture large, terminal; gonothecal pedicel short, on hydrothecal pedicel or on stolon. Medusa released at four-tentacle stage. Nematocysts described by Östman (1979).

2. '*Planktonic*' *colonies.* Floating colonies have been described by several authors (e.g. Van Breemen, 1905; Billard, 1907; Vervoort, 1946*a*, 1959, 1968, 1972). Available evidence suggests that they are benthic colonies which have grown on sand and become detached (see Remarks). Colonies comprise one to several pedicels arising from a basal disc which often (Leloup, 1933) envelops a sand grain, stolons apparently being absent. Pedicels exceptionally long, branching repeatedly, branches often aligned parallel with primary pedicel. Hydrotheca long, narrow, thin walled, terminal cusps as in benthic form. Gonotheca long, smooth walled; rugose and concertinered gonothecae apparently not recorded from free floating material.

Variation. Ralph (1957) found that cooler water increased the number of hydrothecal cusps. Although the species is highly variable there have been few studies of the factors involved.

DISPERSIVE STAGE. A medusa, released at the four-tentacle stage. Umbrella hemispherical or slightly flatter; up to 25 mm in diameter; jelly fairly thin. Velum narrow; stomach short, four-sided; manubrium about 1/6 bell diameter in length, four-lipped. Radial canals 4; gonads elongate to oval, on distal 1/4–3/4 of radial canal but stopping just short of ring canal. Marginal tentacles 16–32 [58 recorded, Kramp, 1919 (= 64)], short, hollow, smooth, with spherical bases. 1–3 closed marginal vesicles between each marginal tentacle and next. Tentacle bases and stomach yellow, yellowish brown, greenish or purple; gonads yellowish. (After Kramp, 1919, 1961; Russell, 1953.)

The relation between hydroid and medusa has not always been understood, and there are still some unsolved problems relating to the nominal species described from the hydroid stage as '*Laomedea gracilis* Sars'.

Böhm (1878), working at Helgoland, worked out the life cycle of *C. hemisphaerica* and his account was quoted by Haeckel (1879 : 187) in his World synopsis; but many years later Mayer (1910 : 267) wrote 'the mature hydroid is not known with certainty, but is probably a *Campanulina* (see Hincks, 1868 : 179)'. Mayer should have quoted Hincks as indicating '*Campanularia raridentata*', now regarded as conspecific with *hemisphaerica.* Hincks' citation in fact referred back to Wright's (1862) description of the hydroid stage under the name *Thaumantias inconspicua*; but Hincks (1852) himself had still earlier seen medusae released (identifying his material as '*Campanularia volubilis* Ellis & Solander'). Hincks thus seems to have been the first to record medusa release in the present species. Du Plessis (1871) also saw medusa release at an early date, but used the combination *Clytia volubilis.* (Notes on the widespread confusion between the species names *volubilis* and *hemisphaerica* are given below.) Mayer's oversight is the more surprising since he quoted Metschnikoff's (1886*b*) description of a polyp reared from the Mediterranean medusa *Clytia flavidula* (Péron & Lesueur, 1810a), which Mayer thought conspecific. The identity of *C. flavidula* is discussed under Remarks.

The later but independent suggestions of Browne (1896 : 488; 1900 : 725–726; Browne & Vallentin, 1904 : 125, 127) that the hydroid of '*Phialidium hemisphaericum*' was '*Campanularia johnstoni*' were supported by Kramp in 1914 (Kramp, 1919 : 93, footnote), some forty years after Böhm and Haeckel wrote and even longer after the suggestions of Du Plessis, Hincks and Wright. The delay parallels that which occurred in the working out of the *Obelia* life cycle (Cornelius, 1977*a*, *b*).

Reproductive season. Medusae occur all through the year in British waters but are most numerous from spring to autumn [Hincks, 1852, as *C. volubilis* (in February); Russell, 1953; J. H. Robson, in Evans, 1978, as *C. gracilis*)]. Lo Bianco (1909, as *Clytia flavidula* and *C. johnstoni*) recorded medusae off Naples from August to October and from January to March.

Distribution. Nearly cosmopolitan in coastal waters (Ralph, 1957; Kramp, 1961), occurring in most of the present area. In European waters the medusa is one of the commonest (Russell, 1953). However, the species was said to be scarce in N Norway by Mathiesen (1928) who cited only two certain records, from Bergen and Hammerfest. It has been reported absent from Greenland (Kramp, 1943; Calder, 1970) although present in Iceland, Spitzbergen, the Faeroes and the Bering Sea (Calder, 1970). 'Planktonic' hydroid colonies have been reported as common in the southern North Sea and off much of the coast of W Africa (Vervoot, 1946*a*, 1959).

Habitat. Usually benthic; intertidal to 150+ m (Crawshay, 1912; Marine Biological Association, 1957; Kramp, 1959; Millard, 1975; BMNH collections). Naumov (1969) reported a lower limit of 300 m but did not cite material. Rees & White (1966) listed a record from 1250 m off the Azores as *C. gigantea*, a species here regarded conspecific; but I have not checked this report.

The species has been found on a wide variety of invertebrate and algal substrates, and there is no regular association. Among the unusual recorded substrates are sand grains (see Remarks) and pelagic cirripedes. There are several records on parasitic copepods themselves on fish (on *Lernaeocera* on *Gadus* by Leloup, 1930*b*; on *Peniculus* on *Mullus*, on *Lernaeenicus* on *Clupea*, and on *Dinematura* on *Cetorhinus* (the Basking Shark), all by Debouteville & Nunes, 1951, 1952). As in *Obelia*, long distance transport would seem to result (pp. 45, 120).

Remarks. Two factors have contributed to the profusion of redescriptions of this species and to the consequent number of synonyms: it is nearly cosmopolitan, and it is highly variable. The combination *Clytia hemisphaerica* was introduced only some fifteen years ago and there is still much use in a detailed analysis of the taxonomic history of the species. There has been confusion with other species and with other genera, and some of the problems have yet to be solved. The nominal species described from the NE Atlantic are considered below, so far as possible in chronological order.

The notes by Stechow (1921*a*, 1923*a*) and Rees & Thursfield (1965) on the nominal species *Sertularia uniflora* Pallas, 1766, were partly misleading. Pallas included in his synonymy Ellis' (1755) plate 14, figure A, Linnaeus' (1758) citing of that plate under the name *Sertularia volubilis*, and Baster's (1762) plate 2, figures 2a, b, d, 3, 4c, e, 7a–c. Ellis' illustration shows a campanulariid hydroid growing on *Hydrallmania falcata* (Linnaeus, 1758). The pedicels were spirally grooved throughout, not annulated top and bottom as in the present species, and had a spherule at the upper end. These two characters indicate that Ellis' material was the species here called *Campanularia volubilis*. Hargitt (1909), Stechow and Rees & Thursfield wrongly supposed Ellis' material to be *C. hemisphaerica*. The name *Sertularia uniflora* Pallas, 1766, was in fact a nom. nov. for *Sertularia volubilis* Linnaeus, 1758, and since both were based on Ellis' illustration *uniflora* is a junior objective synonym of *volubilis.*

The other illustrations cited by Pallas under *S. uniflora*, those of Baster, show in one place (fig. 2A, b) a sharply cusped hydrothecal rim, but nowhere show details of the pedicel. Hence it cannot be determined whether Baster's material was *volubilis* or *hemisphaerica.* Gonothecae were not shown. Maitland (1876, quoted in Vervoort, 1946*a* : 276) referred part of Baster's illustrations (pl. 2, fig. 7A, a) to *Orthopyxis integra* (Macgillivray, 1842), an opinion disagreed with by both Vervoort (1946*a*) and myself as the hydrotheca of *integra* does not have a cusped margin. Nevertheless, I here designate the material shown by Ellis (1755 : pl. 14, fig. A) lectotype of *S. uniflora* Pallas, 1766, to provide formal protection for the name *integra* from possible threat from *uniflora* should Maitland's opinion ever be upheld.

Rees & Thursfield (1965) were further confusing in stating that 'earlier references by Ellis (1755*a*, *b*) [sic] do not distinguish' between *hemisphaerica* and *volubilis.* They omitted the Ellis references from their paper: indeed, I cannot trace relevant papers by Ellis in that year. His only 1755 publication mentioning campanulariids was his book. In this Ellis (1755 : 25) stated clearly that there were two species and illustrated both on his plate 14. Linnaeus and Pallas (op. cit.) were each careful to cite only one of the species when referring Ellis' illustration respectively to their synonymies of *volubilis* and *uniflora.* The other illustrated species (Ellis, 1755 : pl. 14, B) was named *Sertularia syringa* by Linnaeus (1767 : 1311) and is now known as *Calycella syringa,* family Calycellidae (e.g. Cornelius, 1978).

Thus there is little confusion in the early literature; but Rees & Thursfield (1965) were probably correct in stating that the 'hydroid [stage of *C. hemisphaerica*] is recognisable for the first time under the name *Sertularia uniflora:* Ellis, 1768 : pl. 19, fig. 9'. And in this paper Ellis clearly did confuse the two species he had previously illustrated separately. His use of the name *uniflora* in that paper can be regarded as misidentification, not as homonymy. Ellis' (1768) illustrations show clearly the annulated, not spiralled, pedicels of *hemisphaerica*—incidentally slightly unusual in lacking a smooth central portion—and a characteristic 'concertinered' gonotheca. Further confusion might have resulted from Ellis & Solander's (1786) application of the name *Sertularia volubilis* to illustrations clearly of the present species, but the slightly earlier literature just discussed prevents it. However, Hargitt (1909) was not alone among later authors in applying the combination *Clytia volubilis* to the present species.

C. hemisphaerica was placed in the genus *Oceania* Péron & Lesueur, 1810*a* (as *O. flavidula*), by those authors.

Clytia urnigera Lamouroux, 1816, is referred to *C. hemisphaerica* but is discussed here under *Orthopyxis integra* (pp. 64–65).

The combination *Laomedea gracilis* Sars, 1850, has plagued the literature (see also Remarks under *Gonothyraea loveni*); but as noted by Vervoort (1946*a* : 285) the species name should not be used as it is preoccupied by '*Lomedea gracilis*' C. Pickering, in Dana, 1846 : 689 (lapsus pro *Laomedea gracilis*), which I refer to *Obelia dichotoma* (p. 117). I propose the name *Clytia sarsi* nom. nov. in place of *L. gracilis* Sars, 1850 (preocc.). Lectotype material of *L. gracilis* Sars is designated here on page 94. Nevertheless, the name *gracilis* has been widely applied to colonies having long, narrow hydrothecae and smooth gonothecae. But following Ralph's (1957) account of variation in New Zealand populations most authors have regarded '*sarsi*-type' colonies as an extreme variation of *hemisphaerica.* Further evidence was provided by W. J. Rees (in Rees & Thursfield, 1965) who reared a medusa from a *sarsi* ('*gracilis*') colony and found it the same as the medusa *hemisphaerica* s. str. Kühl (1967) regarded '*sarsi*-type' colonies conspecific with those of *hemisphaerica* on more subjective grounds. But Östman (1979) separated the species on the fine structure of the nematocysts (see also p. 42) and the problem is not yet resolved.

There has been some further debate over the degree of affinity between *C. sarsi* (= *L. gracilis* Sars, 1850), and *Campanularia pelagica* Van Breemen, 1905. Some authors have regarded them identical (e.g. Leloup, 1933, 1952; Vervoort, 1946*a*; Naumov, 1960, 1969;

Garcia Corrales *et al.*, 1978); but the validity of *C. pelagica* s. str. has been difficult to assess. (*Campanularia attenuata* Calkins, 1899, from Puget Sound, seems similar.) Among recent authors Vervoort's (1946*a*, 1959, 1968, 1972) descriptions of the *pelagica* 'form' have been important but the possibility has remained open that *pelagica* was simply based on *sarsi* or *hemisphaerica* material which had detached and grown in the plankton. Billard (1917) also had failed to resolve the question but E. T. Browne, A. Kemna and E. Leloup (in Leloup, 1933) thought *sarsi* (*gracilis*) just to be detached, floating colonies of *hemisphaerica.*

Vervoort (1959, as *Laomedea pelagica*) reported that 'floating' colonies occurred in the North Sea and along much of the west coast of Africa, but Millard (1966) referred Vervoort's African coast material to *C. hemisphaerica* without comment. Subsequently Vervoort (1968) reaffirmed his view that *pelagica* was distinct. He had not seen 'intermediate material'; but presumably there is no intermediate environment. Vervoort separated *pelagica* on its slender, gradually narrowing hydrothecae, an undulating cross-section just below the hydrothecal rim and a smooth walled gonotheca. He cautiously noted that two species of *Clytia* medusae had been recorded from the North Sea by Russell (1953) and that these might relate to the two hydroids, *pelagica* and *hemisphaerica.* He subsequently (Vervoort, 1972) retained specific status for *pelagica* but Millard (1975) again referred Vervoort's African coast material to *hemisphaerica.* So the experts were divided. Naumov (1960, 1969) meanwhile had considered *pelagica* distinct but extended its limits slightly further than Vervoort to include *sarsi*-type material with smooth walled gonotheca. Garcia Corrales *et al.* (1978) similarly regarded *sarsi* + *pelagica* distinct from *hemisphaerica*, based on sharper and longer hydrothecal cusps and longer hydrotheca in the former; and like Vervoort (1968) had seen no intermediate material. Other features on which *pelagica* has been distinguished are the frequency of branching and the tendency of the branches to run parallel with the primary stem, noted by Vervoort (1959) but not apparent in all planktonic material; and a smooth, asymmetric gonotheca (e.g. Billard, 1917).

Vervoort (1972 : 91, footnote) drew attention to the report by Sars (1850, 1857; ?repeated in Leloup, 1952) that '*pelagica*' had sessile gonophores. Vervoort cited observations that '*pelagica*-type' material released its medusae and (pers. comm.) now considers that the contrary observations of Sars might have been made on *Gonothyraea loveni* material.

Old and new evidence for uniting *pelagica* with *hemisphaerica* runs as follows. Ralph (1957) showed that smooth gonothecae are not unusual in *hemisphaerica*, and that the length of the hydrotheca and shape of the cusps on the rim vary widely, to an extent which encompasses the three nominal taxa. The *basal discs* (= *Haftplatte* of Kuhn, 1913, and *disque de fixation* of Houvenaghel-Crèvecoeur, 1973; there seems no English equivalent already) of attached *C. hemisphaerica* examined by me seem identical with the 'partie basale' or '*pied . . . globuleuse*' described in planktonic colonies by Billard (1917) and Leloup (1933) under the name *pelagica* (Fig. 9). Also, Leloup showed that the basal discs of these free-floating colonies often contain a sand grain, indicating a benthic origin. Next, the distinctive upward-swept pedicel bases in *hemisphaerica* s. str. seem identical with those described as *pelagica*. Finally, it might have been expected that a hydroid which was habitually planktonic would have some obvious modification to that end; but there seems none.

The relation between the three nominal forms *hemisphaerica*, *sarsi* and *pelagica* is certainly close, and the relation to *johnstoni* is still uncertain (see below). Whether the differences are phenotypic or genotypic cannot yet be decided; but on skeletal and medusa characters it seems best now to interpret the variation as representing a single 'morphological species'. More detailed studies, such as that of Östman (1979) on the nematocysts, might shed further light.

Campanularia volubilis (Ellis & Solander, 1786) sens. Hincks (1852) was the present species. Hincks' account was probably the earliest record of medusa release in *C. hemisphaerica.*

Campanularia johnstoni Alder, 1856*a*, is apparently the earliest available name for the hydroid stage most usually (but subjectively) connected with the medusa on which the present species is based (see Nomenclature, above). It is also the correct species name for the type species of the genus *Clytia* (p. 71). The type series of *Campanularia johnstoni* is mentioned under Material, above, and by Cornelius & Garfath (1980). See also Cornelius (1981).

Phialidium viridicans Leuckart, 1856, is discussed above (p. 71) and on page 86.

Clytia noliformis (McCrady, 1857, as *Campanularia*) was founded on a hydroid which released a *Clytia* medusa lacking gonads when liberated. Kramp (1959, 1961) regarded the lack of gonads on release an important character; and the species has been widely recognized from both hydroid and medusa stages in warm waters throughout the World (references in Fraser, 1944; Kramp, 1961; comment in Rees & Thursfield, 1965). Mammen (1965) gave this name to a medusa he reared but it closely resembled Russell's (1953 : pl. 17, fig. 6) illustration of *C. hemisphaerica*. Mammen's medusa differed only in not showing gonads till 48 hrs old. *C. noliformis* has not otherwise been redescribed since Kramp (1961) wrote and may prove conspecific. Picard (1949) referred medusa and hydroid material from Villefranche to *noliformis* but his specimens, like Mammen's, seemed to differ from *hemisphaerica* only in the short delay in acquiring gonads. Later he included the species in a Mediterranean faunal list, regarding *C. flavidula* Metschnikoff, 1886*a*, and *C. mollis* Stechow, 1919*a*, as conspecific (Picard, 1958*b*). These two species have both been referred to *hemisphaerica* by at least some senior authors; and are discussed in their chronological place below. Rees & Thursfield (1965) referred some Cape Verde material from James Ritchie's collection to *C. noliformis*. They regarded *Campanularia ptychocyathus* Allman, 1888, from the Azores, as conspecific; but Stechow (1925 : 521) treated *ptychocyathus* as dubious.

Campanularia gegenbauri Sars, 1857, was based on a fertile hydroid colony illustrated by Gegenbaur (1854 : pl. 1, figs 1, 1a, as *Campanularia* n. sp.). I concur with Hincks (1868 : 145), Böhm (1878 : 168) and Bedot (1910 : 254) that the species should be referred to *Clytia hemisphaerica*.

Campanularia volubiliformis Sars, 1857, was a name applied to material described as *Campanularia* sp. by Gegenbaur (1854). The shape of the hydrotheca, pedicel and gonotheca illustrated indicate the present species and not *Campanularia hincksii* as suggested by Carus (1844) and Broch (1912*b*). Heller (1868) and Picard (1951*a*) reported further material without description; while Stechow 1919*a* : 70) referred the species to *Orthopyxis*!

Campanularia raridentata Alder, in Hincks, 1861*b*, was referred to *Clytia hemisphaerica* by Billard (1928) and Rees & Thursfield (1965), and provisionally by Vervoort (1968). The synonymy was agreed by Cornelius & Garfath (1980), who alone saw the holotype. The specimen was simply a young colony of *C. hemisphaerica*. Rees & Thursfield wrongly ascribed the original description to 'Alder, 1857'.

Clytia bicophora Agassiz, 1862, originally based on hydroid material from New England, was recorded as a medusa in the Gulf of Trieste by Thiel (1935 : 172, as *Phialidium bicophorum*). But Agassiz' detailed description and clear illustrations appear to represent *C. hemisphaerica*, and *bicophora* can be regarded conspecific. Kramp (1959 : 149) listed other records of *bicophora* as 'uncertain', and indeed Böhm (1878) referred *bicophora* to *C. johnstoni*, which is also regarded conspecific. Kramp (1959, 1961) nevertheless described a medusa under the name *bicophora* and listed references to that species; but the supposed differences from *hemisphaerica* seem unimportant.

Clytia (Platypyxis) cylindrica Agassiz, 1862, was based on both hydroid and medusa material from Massachusetts Bay and Buzzards Bay, North America. The species was referred to *C. hemisphaerica* by Böhm (1878), but to *C. noliformis* (McCrady, 1857) by Bedot (1910 : 348) and Kramp (1961 : 170). (Bedot clearly regarded *Platypyxis* a synonym of *Clytia*, and I concur; see p. 71.) Agassiz' description of *cylindrica* includes no important differences from *hemisphaerica* and like Böhm I regard them conspecific. Vervoort (1968) described new material, and commented on the similarity of *C. elsaeoswaldae* Stechow, 1914. I agree with Vervoort in regarding the Stechow species conspecific.

The combination *Phialidium languidum* (Agassiz, 1862) has been applied to medusae caught off Senegal, but Kramp (1955) referred both the material involved and the nominal species itself to *C. hemisphaerica* (see Kramp, 1933, 1955, 1961, for discussion).

Campanularia ?gigantea Hincks, 1866, was probably based on large *hemisphaerica* hydroid material. The eleven hydrothecae of the holotype well enough preserved for study measured, in mm from diaphragm to tips of hydrothecal cusps, 1·18, 1·26, 1·29 (3), 1·53, 1·62 (2), 1·78, 1·88, 1·91. The wide range is striking, as is the sheer size of the largest; but Hincks was rightly cautious to introduce the name as *?gigantea*. Several authors have referred large material to *gigantea* solely on the basis of size. The pedicels too are long, but the upward curve of the pedicel bases recalls *hemisphaerica* s. str. and continued separation seems uncalled for. Gonothecae have never been reported in this large material. Hincks' (1868) later illustration of the holotype is accurate; and that of Jäderholm (1909), of non-type material, is similar. The material fron N Scotland listed by Rees & Thursfield (1965; BMNH 1964.8.7.75) is *C. hemisphaerica* and is smaller than the holotype of *?gigantea*. The material from Belgium cited by Leloup (1952) seems to have been the same, as does the North Sea material listed by Billard (1928, as *Clytia johnstoni*).

Gastroblasta raffaelei Lang, 1886, was based on a medusa from Naples. The species was provisionally referred to *C. hemisphaerica* by Kramp (1959 : 148).

Clytia flavidula: Metschnikoff, 1886*a*, was a comb. nov. for *Oceania flavidula* Péron & Lesueur, 1810*a*, originally described from medusae collected from Nice. Mayer (1910) referred the species to *C. hemisphaerica* and Russell (1953) concurred. Lo Bianco (1909 : 540) also used the combination *Clytia flavidula*. Kramp (1961 : 65) listed another use of the binominal *O. flavidula*, for *O. armata*, a clavid medusa.

The Mediterranean material referred by Stechow (1919*a*) to *Campanularia serrulata* Bale, 1888 (first described from Sydney), was examined here and found to be simply *Clytia hemisphaerica*; as indeed seems Bale's species, which was described from infertile material. In general agreement, Stepanyants (1979) referred *C. serrulata* to '*Campanularia gracilis*' Sars, 1850, itself regarded conspecific (see above). Picard (1958*b*) recorded the species as Mediterranean without comment.

Campanularia attenuata Calkins, 1899, originally described from Puget Sound, resembles '*Laomedea pelagica* Van Breemen, 1905', and like it should probably be regarded conspecific with *Clytia hemisphaerica*. Material was recorded from Ghana by Buchanan (1957) and it is well known that '*pelagica*-type' colonies occur along the African coast (see above). Although West & Renshaw (1970) recognized the species on the basis of its branched colonies as grown *in vitro* at certain temperatures (see p. 40) further proof of validity seems necessary. *C. attenuata* Stechow, 1919*a*, from Villefranche, is a junior homonym and later in the same paper Stechow (1919*a* : 157) introduced the nom. nov. *Campanularia villafrancensis* instead. However, *villafrancensis* too seems conspecific with *hemisphaerica*.

Campanularia edwardsi Nutting, 1901*b*, based on material from Massachusetts, was redescribed at length by Kubota (1978, as *Clytia*). He provisionally referred *C. edwardsi* to the present species, and I concur.

Clytia simplex Congdon, 1907 : 471–472, figs 14–15, based on material taken off *Sargassum* weed near Bermuda, was reported south of the Azores by Vanhöffen (1910). Fraser (1944), however, referred the species to *C. noliformis* McCrady, 1857, here regarded conspecific with *C. hemisphaerica*; and it seems probable that *C. simplex* too is conspecific.

Clytia obeliformis Stechow, 1914, was based on material from Bergen, Norway. The original illustration shows both hydrotheca and gonotheca typical of *C. hemisphaerica* and the type material, examined here, comprises simply a rather elongate colony of the present species. There is no reason to maintain a separation.

Campanularia acuta Stechow, 1919*a*, was a nom. nov. applied to *C. raridentata:* var. Marktanner-Turneretscher, 1890, based on material from NW France. The variety was originally held to differ from *C. raridentata* s. str. in lacking annulations around the base of the gonotheca; and like that species seems to have been based on *Clytia hemisphaerica* material.

Campanularia brachycaulis Stechow, 1919*a*, was based on a small, infertile colony from Villefranche. The illustrated hydrotheca does not seem to differ from that of *Clytia hemisphaerica*; and I must disagree with Patriti (1970) who referred the species to *Campanularia hincksii.*

Clytia compressa Totton, 1930, was proposed on the basis of the shape of the hydrothecal cusps and of the gonotheca. Ralph (1957) and Vervoort (1968) regarded it conspecific, and I concur.

Stolon growth in the hydroid stage was described by Hale (1964, 1973*a*, *b*).

Clytia hummelincki (Leloup, 1935)

(Fig. 10)

Laomeda hummelincki Leloup, 1935 : 19, fig. 7; Buchanan, 1957 : 360, fig. 11 a–b.
Campanularia hummelincki: Fraser, 1944 : 122, pl. 21, fig. 93; Vervoort, 1966 : 96.
Clytia hummelincki: Deevey, 1954 : 270; Millard, 1966 : 480–481, fig. 14 g–l; Millard, 1975 : 218–220, fig. 72 f–h.

TYPE LOCALITY AND MATERIAL. Isle de Bonaire, West Indies, 0·7 m depth, on dead coral, infertile material on microslide (Fig. 10); Mus. Roy. Hist. Nat. Belg. collection.

OTHER MATERIAL EXAMINED. Fragments of fertile colonies on two microslides, Aghulas Bank, off South Africa (34° 43′ S, 25° 40′ E); South African Museum reg. no. H 2967 (mentioned, Millard, 1966, 1975).

DESCRIPTION OF HYDROID STAGE (partly after Leloup, 1935; Buchanan, 1957; Millard, 1975). Colony a tortuous stolon bearing long hydrothecal pedicels at irregular intervals;

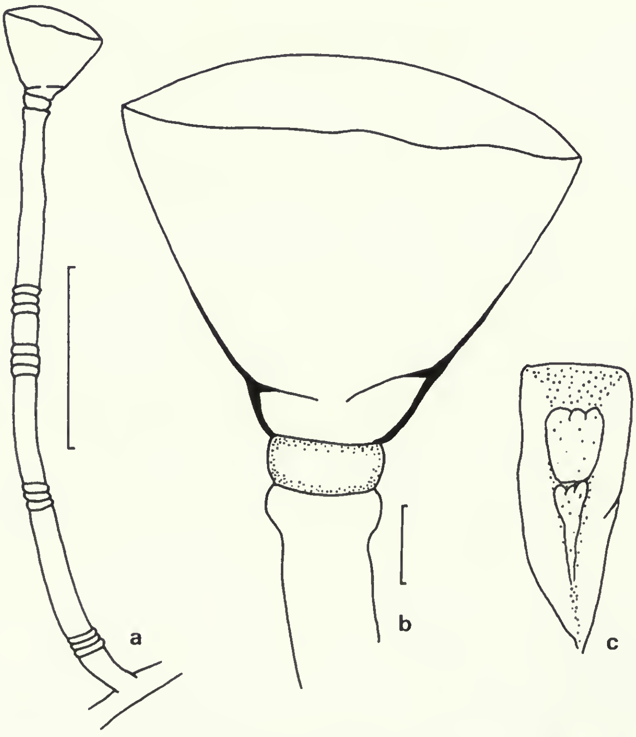


Fig. 10 *Clytia hummelincki.* (a–b) hydrotheca from syntype series, two magnifications. (c) ♀ gonotheca (after Millard, 1975 : fig. 72H). Scales: (a) 50 μm; (b–c) 500 μm.

gonothecae subsessile on stolon. Hydrothecae short, wide, unthickened, length = maximum breadth, tapering sharply towards base which is usually slightly constricted; rim often sloping, even to slightly and irregularly sinuous; diaphragm delicate, oblique in lateral view, either parallel with hydrothecal aperture or sloping in opposite direction; basal chamber small. Hydrothecal pedicel long, smooth or with several basal annulations and up to *c.* five groups of 3–5 annuli along length; sub-hydrothecal spherule present, below which often a slight constriction (see Fig. 10). Hydranth with spherical hypostome and *c.* 20 tentacles. Gonotheca (?♂ = ♀) sessile to shortly stalked, truncate; widest above, tapering below; sometimes asymmetric; aperture probably broad as end; with 1–2 medusa buds, development successive; buds with 4 radial canals and 4 tentacle rudiments (South African material); mature gonotheca and medusa undescribed.

MEASUREMENTS. See Table 2.

Table 2 *Clytia hummelincki* Measurements in μm.

	Caribbean (Leloup, 1935)	Ghana (Buchanan, 1957)	South Africa (Millard, 1966, 1975)
Hydrotheca			
Length	200–240	250	250–400
Breadth (max)	250	240–250	200–420
Length/breadth	*0·8–0·96*	*1·00–1·04*	*0·7–1·36*
Pedicel			
Length	1500–2000	2000	1920–4730
Breadth (max)	40–60		90–150
Gonotheca			
Length			730–1260
Breadth (max)			280–450

DISPERSIVE STAGE. Probably a medusa. Millard (1966, 1975) noted medusa buds with 4 marginal bulbs and so referred the species to *Clytia*. See also Description, Remarks under *C. hemisphaerica* and Dispersive stage under *C. gravieri*.

REPRODUCTIVE SEASON. The only recorded fertile material was collected from Aghulas Bank, South Africa, on 10 February, 1962 (Millard, 1966). The gonothecae contained well developed medusae.

DISTRIBUTION. A little known species, recorded in the NE Atlantic only from Ghana (Buchanan, 1957). Other Atlantic records indicate a wide distribution: West Indies (Leloup, 1935; Vervoort, 1966), Florida Keys and Woods Hole (Deevey, 1954, possibly northernmost record of species) and South Africa (Millard, 1966, 1975).

HABITAT. The few collected colonies have been on *Lepas* (Cirripedia) attached to a buoy, on sublittoral coral debris and on intertidal *Sargassum* weed (Leloup, 1935; Buchanan, 1957; Millard, 1966), indicating a wide substrate range. Recorded depths have so far ranged only from intertidal (Buchanan) to less than 1 m (Millard).

REMARKS. This rarely reported species is clearly widespread in the warmer parts of the Atlantic Ocean. It is retained in *Clytia* following Millard's notes on the developing medusa. Although the species has a sub-hydrothecal spherule it is not transferred to *Campanularia* since that character might be due to convergence (see p. 41). But the affinities of the species remain uncertain and the identity of the medusa might provide better indication.

Clytia islandica (Kramp, 1919)
(Fig. 11)

Phialidium islandicum Kramp, 1919 : 95, pl. 4, figs 11–13, pl. 5, figs 1–2; Russell, 1953 : 294–296, text-figs 180–181; Kramp, 1959 : 149, 215, 218, 221, 222, fig. 190; Kramp, 1961 : 169 (?syn. *Staurostoma laciniatum* var. *hybridum* Le Danois).

TYPE LOCALITY. Coastal waters of Iceland.

DESCRIPTION OF MEDUSA STAGE (Hydroid unknown). Diameter of adult 35–40 mm, umbrellar saucer-shaped, jelly thin; stomach small, cruciform; manubrium reduced, mouth square surrounded by crenulated lips; gonads narrow, along almost whole length of radial canals; tentacles *c.* 200, alternating with statocysts.
Variation. See Russell (1953) and Kramp (1959).

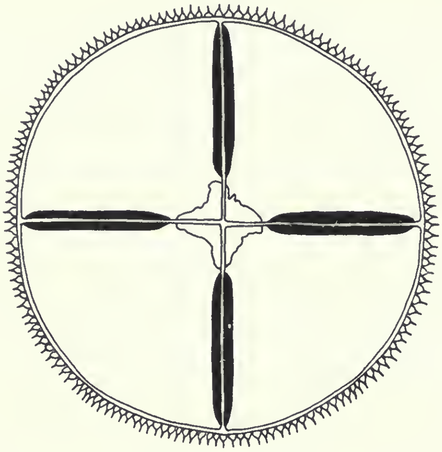


Fig. 11 *Clytia islandica.* Redrawn after Kramp (1959 : fig. 190). Diameter 35–40 mm.

DISTRIBUTION. Reported at least as far south as SW Ireland but records generally more northerly (Russell, 1953). Kramp (1961) cited unconfirmed records from the Bay of Biscay.

REMARKS. Distinguished from the medusa stage of *Clytia hemisphaerica* by: larger diameter (up to 40 mm, not up to 20 mm), flat (not hemispherical) shape, more numerous tentacles [up to *c.* 200, not up to (rarely) 58], usually rather larger gonads and one (not 1–3, usually 2) statocysts between tentacles. The hydroid is not known.

Disuse of the genus name *Phialidium* is discussed above (p. 74). Kramp (1961) referred the genus *Staurostoma* Haeckel, 1879 : 130, to *Staurophora* Brandt, in the family Laodiceidae.

Clytia linearis (Thornely, 1899)
(Fig. 12)

Obelia linearis Thornely, 1899 : 453, pl. 44, fig. 6.
Campanularia gravieri Billard, 1904*a* : 482, fig. 1; Billard, 1907 : 171–172.
?*Clytia geniculata* Thornely, 1904 : 112–113, pl. 3, figs 4, 4a.
Campanularia ?obliqua Clarke, 1907 : 9, pl. 5, figs 1–4.
Clytia linearis: Stechow, 1913 : 66–69, figs 23–25; Hirohito, 1977 : 14–20, fig. 4a–j (syn. *Campanularia gravieri* Billard; *Clytia hendersonae* Torrey, 1904; *C. alternata* Hargitt; *Laomedea bistriata* Leloup).
Clytia alternata Hargitt, 1924 : 483, pl. 2, fig. 7.
?*Clytia (?)foxi* Billard, 1926 : 93–94, fig. 9A–B.

Laomedea (Obelia) bistriata Leloup, 1931*a* : 4, figs 8–11.
Clytia gravieri: Billard, 1938 : 429–432, figs 1–3, ?fig. 4 (syn. *C. alternata* Hargitt, *Laomedea bistriata* Leloup); Picard, 1955 : 185–186; Millard & Bouillon, 1973 : 51–54, fig. 7e–g (syn. *Obelia striata* Clarke, 1907; *C. serrata* Millard, 1958); Millard, 1975 : 215–217, fig. 71 F–H (syn. *Obelia striata* Clarke, 1907); Garcia Corrales, Inchaurbe & Mora, 1978 : 29–30, fig. 12.
Clytia obliqua: Picard, 1950 : 51–52.
Campanularia (Clytia) gravieri: Vervoort, 1967 : 50–52, fig. 16 (syn. *Clytia alternata* Hargitt; *Laomedea bistriata* Leloup).

TYPE LOCALITY. Blanche Bay, New Britain, Bismarck Archipelago. Material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Campanularia obliqua* Clarke, 1907, infertile colonies on sertularian hydroid, in spirit, 'Perico Island', Gulf of Panamar, coll. r.v. 'Albatross'; Smithsonian Institution cat. no. 29616.

Clytia alternata Hargitt, 1924, fertile colonies preserved on microslide, Port Galero, Mindoro, Philippines; Smithsonian Institution cat. no. 42644 (Fig. 12).

OTHER MATERIAL EXAMINED. None.

DESCRIPTION OF HYDROID STAGE (partly after Thornely, 1899; Billard, 1904*a*, 1938; Stechow, 1925; Picard, 1951*a*; Vervoort, 1967; Millard & Bouillon, 1973; Millard, 1975; Hirohito, 1977). Colonies both stolonal and erect. When erect branching sympodially, up to *c.* 10 hydrothecae in extent, to 20 mm. Hydrothecal pedicels finely ringed throughout (6–37, usually *c.* 20) or with smooth central portions; distal pedicels shorter than proximal. Internodes of erect stems arcuate, narrowly ringed basally. Hydrothecae long, sides parallel to slightly divergent, often with slight asymmetric bulge; with 8–16 long narrow marginal cusps recalling those of *Clytia paulensis* and *Obelia bidentata* but each with internal

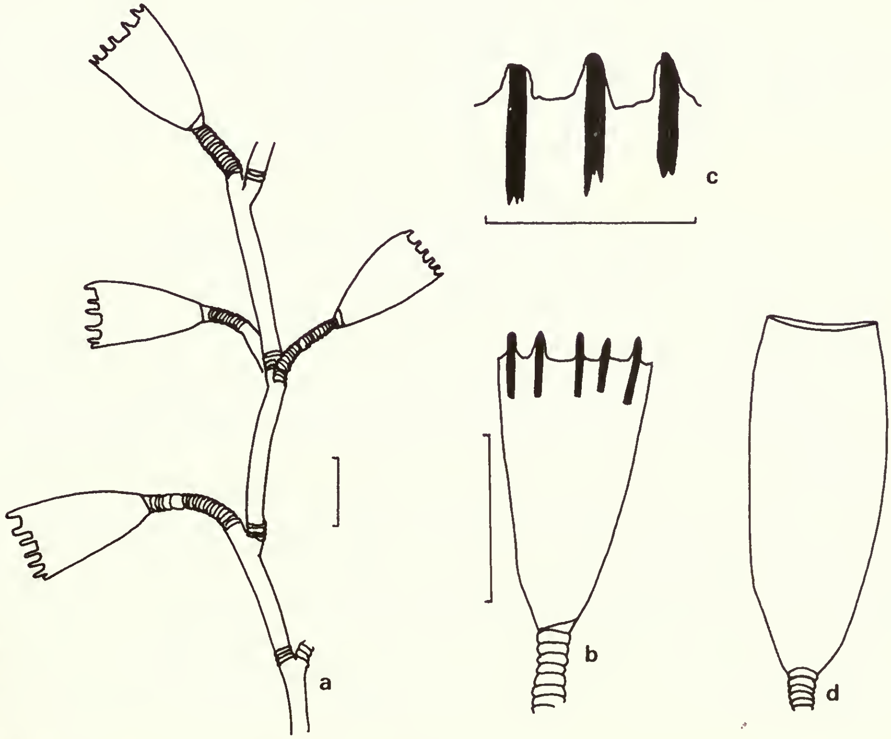


Fig. 12 *Clytia linearis.* The specimen illustrated is a syntype of *C. alternata* Hargitt, 1924, here regarded conspecific. (a) part of colony. (b–c) hydrotheca and part of rim. (d) ♀ gonotheca. Scales: (a) 500 μm; (b) 250 μm; (c–d) 500 μm.

stiffening strip reaching to tip and extending downwards sometimes to middle of hydrotheca; intervening bays rather wide and square, bulging out; diaphragm usually oblique but sometimes transverse. Hydranth with 12–15 tentacles (in holotype specimen of *C. alternata* Hargitt). Mature gonotheca (?♂ = ♀) elongate, on 2–3 ringed pedicel, either on stolon or on erect shoot in axil; widest in centre, tapering below and usually above; one-flapped circular deciduous operculum; young gonotheca shorter, more sharply truncated. Gonophore with one or more rows of developing medusae; pre-release medusae with hemispherical umbrella and four marginal tentacles.

Variation Hydrothecal length varies greatly, at least from 400 μm to 1100 μm (Millard, 1975). Internodes and pedicels are shorter in upper parts of the colony (Hirohito, 1977). Hirohito found little difference between Red Sea and Japanese specimens, indicating a rather constant phenotype. Hydrothecal pedicels were on the whole shorter in the Japanese specimens, but gonothecae were similar in size. Billard (1938) reported that the embayments between the hydrothecal cusps are often distorted in preserved material due to lateral folding.

DISPERSIVE STAGE. A medusa, with hemispherical umbrella and four marginal tentacles on release; earliest stage identical with newly liberated *Clytia hemisphaerica* medusa, even in cnidom according to Picard (1951*a*). Adult medusa not described (Millard, 1975). Russell (1953) noted that the Mediterranean medusa *Phialidium viridicans* Leuckart, 1856, might prove valid. It might follow that *Clytia linearis* is its hydroid, but evidence is only circumstantial and the hydroid stages of *C. hummelincki* and *C. paulensis* must also be considered. '*P. viridicans*' is here provisionally referred to *C. hemisphaerica*.

DISTRIBUTION. Circumglobal in tropical to warm shallow seas (Millard & Bouillon, 1973; Hirohito, 1977) extending northwards in the Atlantic Ocean at least to the south coasts of France ('extremely common' intertidally at Banyuls, Picard, 1951*a*) and Spain (10–20 m off Alicante, Garcia Corrales *et al*., 1978). Billard (1907) recorded the species south of Madeira; Picard (1955) from Algeria; Rees & Thursfield (1965, as *C. striata*) from the Cape Verde Is and Rees & White (1966, as *C. striata*) from the Azores. Vervoort (1967) gave a list of known Indo-Pacific localities; and some possible records under other specific names are discussed below.

HABITAT. On cirripede and pteropod shells and on other hydroids (Billard, 1904*a*; Vervoort, 1967; Millard & Bouillon, 1973; Millard, 1975; Hirohito, 1977); also on intertidal rocks (Picard, 1951*a*). Intertidal (Picard) to 110 m (Billard, 1907; Millard).

REMARKS. Ritchie (1907) recorded material from the Azores as *Clytia geniculata* Thornely, 1904, a name originally applied to specimens from Sri Lanka. Rees & Thursfield (1965) tentatively thought *C. geniculata* conspecific with *C. striata* (Clarke, 1907), which Millard & Bouillon (1973) and Millard (1975) referred to the present species. But Hirohito (1977) described what he considered undoubted *C. striata* material (on a pteropod) and considered the species valid.

Picard (1950) assigned material from near Marseille to *Clytia ?obliqua* Clarke, 1907) but that species seems identical with *Clytia linearis*. Clarke based the distinction merely on the angle of slope of the hydrothecal cusps. The type material of *C. obliqua*, examined here, does not otherwise differ from the original description of *C. gravieri*.

The type material of *Clytia alternata* Hargitt, 1924, was examined also by Hirohito (1977). As he stated, it resembles the description of *C. linearis* so closely that the two species can be regarded conspecific. *C. foxi* Billard, 1926, was based on slight differences and may also be the same species. Vervoort (1967) drew attention to the close similarity between *C. alternata* and *C. gravieri* Billard, 1904, which also seems conspecific. Billard (1938) had earlier thought them conspecific along with *Laomedea bistriata* Leloup, 1931*a*. He saw four marginal tentacle bulbs in the pre-release medusa and hence assigned the species to *Clytia*. Detailed discussion of several Pacific forms was provided by Hirohito.

Clytia mccradyi (Brooks, 1888*b*)
(Fig. 13)

Oceania sp. Brooks, 1888*a* : 29–30.
Epenthesis mccradyi Brooks, 1888*b* : 147–162, pls 13–15; Sigerfoos, 1893 : 106.
Oceania mccradyi: Mayer, 1900 : 50, pl. 21, figs 56–59.
Phialidium mccradyi: Mayer, 1910 : 271–272, pl. 34, figs 2–3, pl. 35, figs 1–3; Kramp, 1959 : 149; Kramp, 1961 : 170; Bougis, 1963 : 2,2–2,3, pl. 9, fig. 2.
Further references were given by Mayer (1910) and Kramp (1961).

TYPE MATERIAL AND LOCALITY. Green Turtle, 1886, and Nassau, 1887, Bahamas (medusa stage only); material not located.

MATERIAL EXAMINED. None available.

DESCRIPTION OF HYDROID STAGE. The identity of the hydroid stage is unclear. The species was originally based on mature medusae collected from the plankton. Brooks (1888*b*) later saw young medusae released from a hydroid colony and, identifying the young medusae as the same species as the adults earlier described, concluded he had found the hydroid. Mayer (1910) was sceptical. Brooks' description of the hydroid did not differ from the hydroid of *C. hemisphaerica.* The description included stolonal gonothecae with lateral constrictions characteristic of the better known *hemisphaerica.* Only Brooks has reported a conventional hydroid stage. Others (Sigerfoos, 1893; Mayer, 1910; Bougis, 1963) have described a much reduced hydroid stage comprising only hydroid blastostyles within gonothecae, attached to the gonad of the medusa.

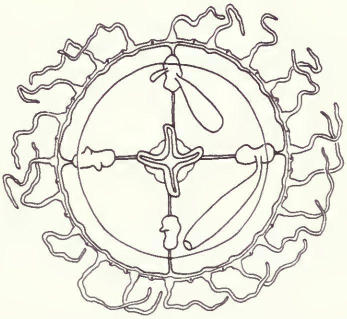


Fig. 13 *Clytia mccradyi.* Redrawn after Mayer (1910 : pl. 35, fig. 1). Diameter *c.* 15 mm.

DISPERSIVE STAGE. A medusa. The following description is after Brooks (1888*b*) and Mayer (1910). Bell shallow, *c.* 15 mm diameter, less than half as high as broad, flexible; stomach short, less than 1/8th as long as diameter of bell, quadrate, with four simple, slightly recurved lips; gonads short, oval, about mid-way between axis and bell margin; velum well developed; 16–24 long, contractile marginal tentacles (type material had 16 only), 'many times as long as diameter of bell', each with statocyst at base; 8–16 other marginal statocysts; 1–4 (?4+) gonothecae borne on one to all of the gonads in many individuals. Gonads of medusa develop either eggs or sperm, or into hydroid blastostyles which produce medusae direct (details in Sigerfoos, 1893 and Mayer, 1910). 4–8 tentacles on release (Brooks, 1888*b*).

REPRODUCTIVE SEASON. Brooks (1888*b*) recorded fertile hydroid material in June, 1887, at Nassau, Bahamas; Mayer (1910) in July at Tortugas, Florida. Medusae from April to July (Mayer).

DISTRIBUTION. In the eastern North Atlantic I know of only one record: Villefranche, S France, found 'from time to time' (Bougis, 1963). Reported elsewhere in the World from the Bahamas and Florida (Kramp, 1959, 1961).

HABITAT. Brooks (1888*b*) reported the 'free' hydroid stage on algae in the harbours of Nassau and Green Turtle, Bahamas.

The hydroid stage is at least sometimes partially suppressed and attaches to or grows on the medusa. Thus the species seems adapted to an oceanic existence and might be found away from coastal waters. Possibly the isolated record from the Mediterranean is evidence of a natural trans-atlantic dispersal.

REMARKS. The unusual life cycle of this species has been checked by at least three independent workers (Sigerfoos, 1893; Mayer, 1910; Bougis, 1963) since the original description by Brooks (1888*b*). Brooks alone claimed to have found a benthic hydroid stage, but Mayer evidently doubted his observation. Although Mayer studied live medusae of the species closely, Brooks' account is explicit and suggests strongly that the benthic hydroids he described were of this species. At the time Mayer wrote such plasticity in the life cycle of a single hydromedusa species would have been regarded unusual and requiring more rigorous proof than today, when several such examples are known (summary in Naumov, 1969).

Brooks stated that the medusa has either 4 or 8 tentacles on release, a departure from the unvarying four usually considered normal in this genus (see p. 42).

Clytia paulensis (Vanhöffen, 1910)

(Fig. 14)

Campanularia paulensis Vanhöffen, 1910 : 298, fig. 19.
Clytia ulvae Stechow, 1919*a* : 47–48, fig. N.
Clytia paulensis: Stechow, 1923*a* : 110, fig. N; Philbert, 1935*b* : 25–26, fig. 4; Picard, 1955 : 186; Millard, 1966 : 481–483, fig. 15 (?syn. *C. ulvae* Stechow, 1919*a*); Millard, 1975 : 221, fig. 73a–d.
Obelia paulensis: Naumov & Stepanyants, 1972 : 37, fig. 2a–b.

TYPE LOCALITY AND MATERIAL. Shallow water in crater lagoon of St Paul Island, S Indian Ocean (38° 40′ S, 77° 34′ E), 26 Apr 1903, on *Sertularella polyzonias* (Linneaus, 1758), coll. Deutsche Südpolar-Expedition 1901–1903; material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Clytia ulvae* Stechow, 1919*a*, infertile colony on *Ulva* (green alga), Marseille, microslide preparation; Munich Zoological Museum. Also 1 non-type specimen, 'Valdivia' sta. 100 (S Africa), det. E. Stechow as *C. ulvae*; MZM.

OTHER MATERIAL EXAMINED (All BMNH material is listed. None is fertile.). Breakwater at S end of Landguard Pt, Felixstowe, Suffolk, SE England, ELWS, Sep–Oct 1976, infertile colony on *Crisia* sp. (Bryozoa) itself on *Tubularia indivisa* Linnaeus, spirit + 1 microslide preparation, coll. & det. R. G. Hughes; 1977.5.7.2. Off Berry Head, Tor Bay, Devon, SW England, *c.* 15 m, Mar–Jun 1973, infertile colony on *Nemertesia* sp., spirit + 1 microslide preparation, coll. R. G. Hughes; 1973.8.13.1 (see Remarks; mentioned, Hughes, 1975 : 291). Off Berry Head, *c.* 15 m, summer 1974, infertile colony on *Nemertesia* sp., co-epizoic with *C. hemisphaerica*, spirit + 1 microslide preparation, coll. & det. R. G. Hughes; 1977.5.7.1 (Fig. 14). Mewstone Ground, near Plymouth, Devon, Oct 1899, infertile colony on *Laomedea flexuosa*, 1 microslide preparation, coll. Marine Biological Association of U.K., ex E. T. Browne colln; 1961.11.14.16 (see Remarks). R. Rance, nr St Malo, NW France, infertile colony on *Hydrallmania falcata* (Linnaeus, 1758), spirit + 2 microslide preparations, coll. M. Philbert; 1935.7.10.1 (?mentioned, Philbert, 1935*b*). Sta. SCD 258 W, Univ. Cape Town Ecol. Survey, 14 Jul 1961, infertile colonies on *Obelia dichotoma*, spirit + 1 microslide preparation, pres. N. A. H. Millard; 1962.6.18.9.

DESCRIPTION OF HYDROID STAGE. Colony stoloniferous, comprising a tortuous, branched, mostly unringed stolon from which usually unbranched pedicels arise at intervals. Pedicels long, occasionally branching as in *C. hemisphaerica* with similar upward-curved bases bringing branches approximately parallel with main pedicel; annulated basally, below hydrotheca and sometimes centrally, forming 1–2 smooth central portions. Hydrotheca

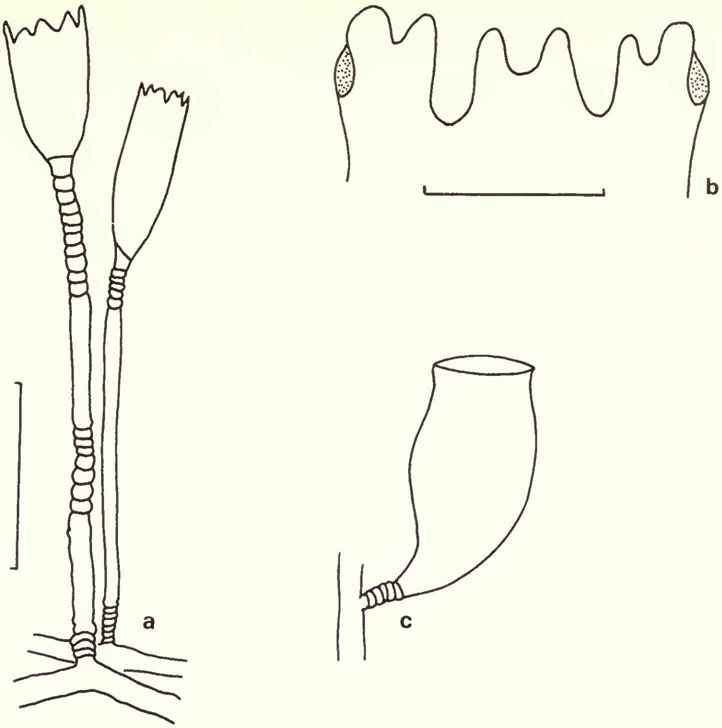


Fig. 14 *Clytia paulensis.* (a) single hydrotheca on pedicel (right) adjacent to same of *C. hemisphaerica* (left), SW England; 1977.5.7.1. (b) part of (a), right hand specimen, enlarged. (c) gonotheca (after Millard, 1975 : fig. 73D). Scales: (a, c) 500 μm; (b) 100 μm.

rather longer than in *C. hemisphaerica*, length : breadth ratio usually 3–4, exceptionally $1\frac{1}{2}$; 7–11 rounded bimucronate cusps; flared appearance immediately below rim resulting from outward bulging of larger embayments; diaphragm oblique; longitudinal folds in hydrothecal wall in microslide preparations can look like striations (Millard, 1975) but are artefacts. Hydranths in present material with 16–22 tentacles. Gonotheca (not seen) ?♂ = ♀, cylindrical, tapering gradually below and slightly above, smooth (after Stechow, 1923*a*; Philbert, 1935*b*; Millard, 1975); borne on stolon on short annulated pedicel. 1–3 medusa buds per blastostyle, pre-release medusa with 4 tentacle buds (Millard, 1975); free medusa not yet described. *Variation.* Cusps on hydrothecal rim variable in both length and breadth; always rounded in present material. Embayments between cusps irregular in depth so that adjacent ones are sometimes similar, obscuring bimucronate condition. Hydrotheca length : breadth ratio usually 3–4 but Millard (1966) gave $1\frac{3}{4}$–$3\frac{1}{4}$, once $1\frac{1}{2}$ (BMNH 1935.7.10.1). Angle of slope of diaphragm variable.

MEASUREMENTS. See Table 3.

DISPERSIVE STAGE. A medusa. Advanced embryos still in the gonotheca have been widely reported as having 4 tentacle buds, as they have in other *Clytia* species, but the free medusa has yet to be described. See also Dispersive Stage under *Clytia linearis.*

REPRODUCTIVE SEASON. No information.

DISTRIBUTION. A widespread, warm water species recorded in the N Atlantic north to Suffolk, SE England. However, *C. paulensis* has been found at only three English localities (present material). Fertile material was reported as 'very common' near St Malo, NW France (Philbert, 1935*b*) but all the English material has been infertile.

Table 3 *Clytia paulensis* Measurements in μm.

	NW France (1937.7.10.1)	NW France (Philbert, 1935*b*)	South Africa (Millard, 1966, 1975)	S Indian Ocean (holotype; Vanhöffen, 1910)
Hydrotheca				
Length	220–350		300–720	360–400
Breadth (max)	130–150		130–330	200
Pedicel length	550–900		500–1800	
Gonotheca (?♂ = ♀)				
Length		900–950		
Breadth (max)		330–410		
Aperture diameter		290		
Pedicel length		50–90		

Other European records are 'the Mediterranean' (Picard, 1958*b*), Naples (Riedl, 1959) and the Glénan Isles, NW France (Fey, 1969); but not the Roscoff area (Teissier, 1965; L. Cabioch, pers. comm.).

HABITAT. Lower shore (present material) to 200 m (Stechow, 1923*a*; Riedl, 1959; Mediterranean); 0–138 m, once 384 m (Millard, 1975, 1977; S Africa). Tolerant of reduced salinity at least as low as 17‰ (Calder, 1976). Usually recorded epizoic on hydroids and other inert animal substrates. The following have been reported: *Laomedea* sp., *Clytia hemisphaerica* (as *C. gracilis*), *Dynamena* sp., *Halecium beanii* Johnston, 1838, *Nemertesia antennina* (Linnaeus, 1758), *Pennaria disticha* sensu Brinckmann-Voss, 1970, *Sertularella* sp. and spines of an echinoid, *Cidaris* sp. (as *Dorocidaris* sp.) (all by Stechow, 1923*a*); *Sertularia cupressina* Linnaeus, 1758, and *Halecium beanii* (by Philbert, 1935*b*); *Hydrallmania falcata* (Linnaeus, 1758), *Obelia dichotoma* and a bryozoan, *Crisia* sp. (present material); and *Nemertesia* sp., *Tubularia* sp. and *Scrupocellaria scruposa* (Bryozoa) in Suffolk and Essex, SE England (by R. G. Hughes, pers. comm.).

REMARKS. The four tentacle buds of the pre-release medusa and the close similarity to *C. hemisphaerica* indicate that *paulensis* is correctly referred to *Clytia*. *C. paulensis* was placed in *Obelia* by Naumov & Stepanyants (1972) because the material they saw was 'strongly branched' but this seems slim reason. Stepanyants (1979) later referred *C. paulensis* to '*Obelia bicuspidata*' Clarke, 1875, a conclusion with which I cannot agree (see notes under *O. bidentata*, p. 117).

The earlier Torbay material listed above, collected in 1973, was the first to be recorded from the British Isles. E. T. Browne's Plymouth material had been collected in 1899 but was overlooked. Browne first identified it as *Campanularia raridentata* Alder, here referred to *Clytia hemisphaerica*; but in 1927 added a note doubting his determination (E. T. Browne ms notebooks **13** : 148–149; Zoology Library, BMNH). The material came to the BMNH as part of the E. T. Browne bequest and was re-identified by the then curator as '*Clytia gracilis* Sars'. The hydrothecal rims, with their rounded bimucronate cusps, clearly differ from those of *C. gracilis* s. str. auct. and the specimen resembles *C. paulensis* in all respects. Although Browne regarded the material as something unusual in 1899 *C. paulensis* was not described until 1910, and he may well have been the first in the World to collect this species.

The type material of *Clytia ulvae* Stechow, 1919*a*, from Marseille, has a bimucronate hydrothecal rim and is undoubtedly *C. paulensis*. Nevertheless, Stechow was among the first to collect *C. paulensis* from Europe and to recognize it as different from *C. hemisphaerica*.

Clytia paulensis is perhaps difficult to identify. It differs from *C. hemisphaerica* in its bimucronate hydrothecal rim, its slender hydrotheca and pedicel and, so far as is known, its consistently smooth gonotheca. Both species are widespread in the World. But in European waters *C. paulensis* has yet to be found north of Suffolk, SE England, whereas *C. hemisphaerica* ranges much further north. Other west European Campanulariidae having bimucronate hydrothecal rims are *Obelia bidentata* and *Laomedea neglecta* which produce taller colonies and branch differently.

Clytia incertae sedis

Two *Clytia* medusae, with 5 and 6 radial canals and diameters of 8 mm and 13 mm respectively, were taken in the southern Adriatic Trough on 9 August, 1969. They were referred to *Phialidium pentata* Mayer, 1900, by Schmidt & Benovič (1977), making the first NE Atlantic record of that species. Kramp (1961) had referred '*P. pentata*' to *Phialidium folleatum* McCrady, 1857 (= *Clytia folleata*) but there remains a possibility that both are abnormal variants of *C. hemisphaerica*. Indeed, Schmidt & Benovič considered: 'It might be possible that all [recorded] specimens [of *pentata, folleata* and also *P. gardineri* Browne, 1904] are abnormal forms of *C. hemisphaerica*'. I concur with their conclusion that more material is needed to resolve these problems.

Leloup (1940 : 21, as *Laomedea*) recorded *Campanularia kincaidi* Nutting, 1899, from the Azores, at 1187 m depth, without description or comment. The record was repeated by Rees & White (1966 : 277, as *Obelia*). The only previous record from the Atlantic was of two colonies from the Caribbean, also by Leloup (1935 : 20). In the absence of more definite indication it seems best to omit the species from the present survey. The nominal species was provisionally referred to *Clytia* by Cornelius (1975*a* : 280).

Subfamily **OBELIINAE** Haeckel, 1879

Obelidae Haeckel, 1879 : 163 (part).
Obelinae: Mayer, 1910 : 231 (part); Russell, 1953 : 296.

NOMENCLATURE. The root of the subfamily name is *Obelia*, and the spelling Obelinae is incorrect.

DIAGNOSIS. Campanulariidae with erect hydrocaulus and true hydrothecal diaphragm; no sub-hydrothecal spherule; stolon not anastomosing; medusa liberated but reduced (*Obelia*), or vestigial and retained (the rest).

TYPE GENUS. *Obelia* Péron & Lesueur, 1810*a* (by present designation).

SCOPE. The genera *Gonothyraea* Allman, 1864*a*, *Hartlaubella* Poche, 1914, *Laomedea* Lamouroux, 1812 and *Obelia* Péron & Lesueur, 1810*a*.

REMARKS. The subfamily name is the oldest available. The Obeliinae was recognized also by Mayer (1910) and Russell (1953), who like Haeckel based their classifications on the medusa stage alone. All the included genera occur in the eastern North Atlantic and are defined below.

Genus ***GONOTHYRAEA*** Allman, 1864*a*

Gonothyraea Allman, 1864*a* : 374.
Gonothyrea auct. (laspus pro *Gonothyraea*).
Campanularia, Laomedea and *Obelia* part, auct. (see Remarks).

TYPE SPECIES. *Laomedea loveni* Allman, 1859*a*; designated by Millard (1975). The originally included species were *L. loveni*, *Campanularia geniculata* sensu Lister (= *G. loveni*; see Cornelius, 1977*a* : 47) and *L. gracilis* Sars. The last named was based on a mixed series comprising what was probably *Clytia hemisphaerica* (hydroid) and *G. loveni*, but following designation of lectotype material (p. 94) it is now subjectively referred solely to *C. hemisphaerica*.

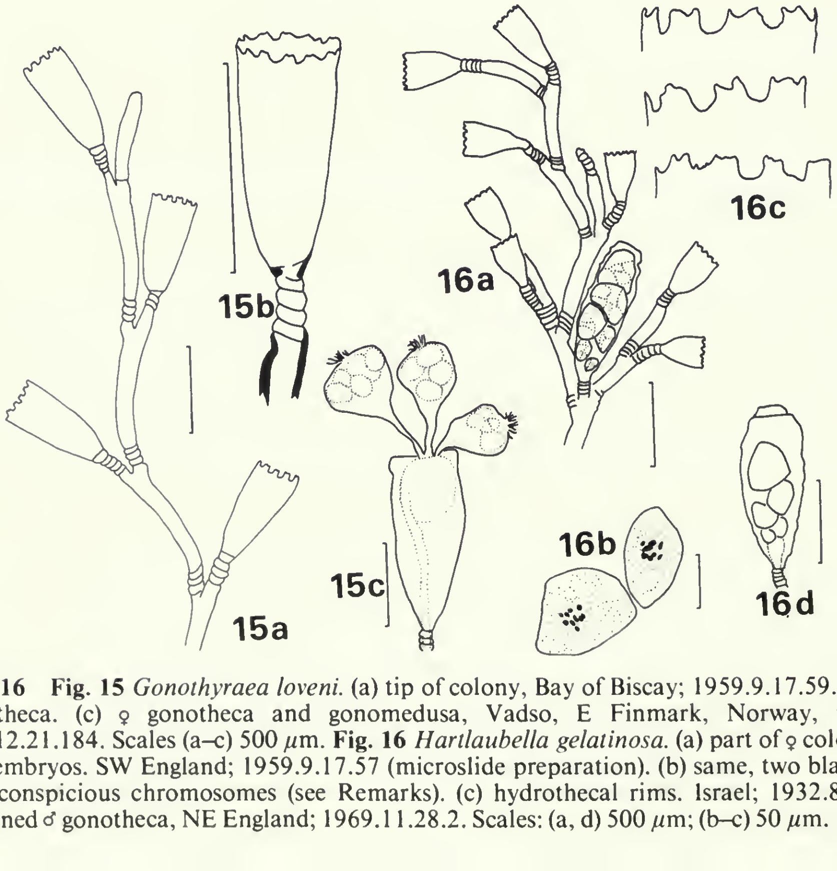
DIAGNOSIS. Campanulariidae forming upright, branched colonies; stem flexuose; hydrothecae tubular, pedicellate, alternate; diaphragm present; no sub-hydrothecal spherule; gonophore a gonomedusa.

REMARKS. I have discussed elsewhere the past confusion between *G. loveni* and nominal species of *Campanularia, Laomedea* and *Obelia* (in Cornelius, 1977*a*). This confusion probably delayed by some decades the discovery of the alternation of generations in medusoid coelenterates; and, it can be claimed, in other animal groups.

Gonothyraea loveni (Allman, 1859*a*)
(Fig. 15)

Laomedea gracilis Sars, 1857 : pl. 2, fig. 4 only (not pp. 51–54, nor figs 1–3, 5, = *Clytia hemisphaerica,* q.v.).
Laomedea loveni Allman, 1859*a* : 138–140.
Gonothyraea (Laomedea) loveni: Allman, 1864*b* : 376.
Gonothyraea hyalina Hincks, 1866 : 297–298; Hincks, 1868 : 184–185, pl. 35, fig. 2.
Gonothyraea loveni: Hincks, 1868 : 181–183, pl. 25, fig. 2.
Obelia loveni: Naumov, 1960 : 264–265, fig. 152 (syn. *G. hyalina* Hincks); Naumov, 1969 : 285–287, fig. 152 (syn. *G. hyalina* Hincks).

NOMENCLATURE. Bedot (1912 : 294; 1916 : 107) listed but two uses of the combination *Obelia hyalina*, and none of *O. loveni*, in his synoptic works (1901–1925). *Obelia hyalina* Clarke, 1879, and *O. hyaliana* Vannucci, 1955, are different nominal species.



Figs 15–16 **Fig. 15** *Gonothyraea loveni.* (a) tip of colony, Bay of Biscay; 1959.9.17.59. (b) same, hydrotheca. (c) ♀ gonotheca and gonomedusa, Vadso, E Finmark, Norway, intertidal; 1912.12.21.184. Scales (a–c) 500 μm. **Fig. 16** *Hartlaubella gelatinosa.* (a) part of ♀ colony. Note large embryos. SW England; 1959.9.17.57 (microslide preparation). (b) same, two blastomeres. Note conspicious chromosomes (see Remarks). (c) hydrothecal rims. Israel; 1932.8.13.1. (d) unopened ♂ gonotheca, NE England; 1969.11.28.2. Scales: (a, d) 500 μm; (b–c) 50 μm.

TYPE LOCALITY AND MATERIAL. Firth of Forth, Scotland (Allman, 1859*a* : 137); material not located.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Gonothyraea hyalina* Hincks, 1866, syntypes, Shetland Is, Scotland, several colonies in spirit, coll. J. G. Jeffreys, on '*Tubularia, Halecium*, etc.', ex Hincks colln; 1899.5.1.157.

OTHER MATERIAL EXAMINED. BMNH collection, about 80 specimens.

DESCRIPTION. Colony erect, stem monosiphonic, delicate, variably flexuose, internodes usually slightly curved, irregularly branched, up to *c.* 100 mm. Annuli above origins of branches. Hydrothecal pedicels usually annulated throughout but smooth central portion frequent; usually tapering distally to roughly half proximal diameter. Hydrotheca cylindrical, campanulate, length $1\frac{1}{2}$–3 times maximum breadth; rim delicate, slightly outturned, castellate, raised portions often notched (Fig. 15); often longitudinal folds in hydrotheca. Hydranth with 20–25 tentacles; branched tentacles recorded but rare (Hamond, 1957); hypostome spherical. Gonotheca (♂ narrower than ♀, otherwise similar; Miller, 1973) cylindrical, truncated above, tapering below. Conspicuous sporosacs or ova develop internally and later extrude up to four together as tentaculate, sub-spherical reduced medusae termed gonomedusae (formerly called meconidia; see Dispersive stage).
Variation. Internode length and curvature, length of hydrotheca and the degree of tanning and translucency of the perisarc are all variable.

DISPERSIVE STAGE. A planula larva. The reduced medusa is retained until after the planulae have escaped. It does not swim but simply drops off. Ellis (1756*a*, *b*, *c*, 1767, but not 1755; see Cornelius, 1977*a*) recorded that the 'released' gonomedusae exhibited strong tentacle movements and adopted a 'worm-like' shape, but his observations seem not to have been repeated.

The gonomedusae were interpreted as highly developed sporosacs by Allman (1859*a*) who coined for them the long standing term meconidia. But Goette (1907) and more recently Miller (1973) have shown that they are actually reduced medusae. Miller introduced the preferable term gonomedusae. Wulfert (1902) provided a summary of early reproductive studies on this species.

REPRODUCTIVE SEASON. Published records suggest that in the English Channel and southern North Sea the species breeds almost throughout the year (Mar–Sep, Hamond, 1957; Jan–Apr & Sep–Nov, Marine Biological Association, 1957; May–Aug & Oct–Nov, Teissier, 1965); but an intertidal population which I studied in 1974 in Sussex, SE England, bore gonomedusae only during the first two weeks of April. Some of the published records might refer to colonies with developing gonothecae, or with empty ones.

Fertile gonothecae were reported at Naples from January to May and in September by Lo Bianco (1909).

DISTRIBUTION. Widespread in suitable habitats and often common. Occurs throughout western Europe north to W Greenland (but not E), Iceland, Faeroes, Spitzbergen, Barents Sea, Murman coast and White Sea (Mathiesen, 1928; Kramp, 1929, 1938; Calder, 1970). In the Baltic *G. loveni* is said to penetrate as far as Helsinki in the Gulf of Finland and the Aland Isles in the Gulf of Bothnia (Linko, 1911; Stechow, 1927; Naumov, 1969). It has been recorded from the Mediterranean Sea (Picard, 1958*b*; Riedl, 1959) and Black Sea (Naumov, 1969); and on the Atlantic coast from W France and Morocco (Billard, 1927; Patriti, 1970).

Millard (1975) recorded the species in South Africa only from Cape Town docks and considered this and other Southern Hemisphere records to result from transport by ships. Hence *G. loveni* might be found further south than Morocco. Rees & White (1966) listed a dubious old Azores record from the unusual depth of 845 m.

HABITAT. Intertidal, usually in pools, and offshore. Naumov (1960, 1969) gave a normal depth range of 0–30 m, with an extreme lower limit of 200 m; and Mathiesen (1928) similarly gave 6–200 m. The BMNH material falls within these limits. The record at 845 m off the Azores listed by Rees & White (1966) is much deeper, and needs confirmation. *G. loveni* is tolerant of reduced salinity at least to 12‰ (Calder, 1976). It has been recorded on a variety of animal, plant and inorganic substrates (Hincks, 1868; Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965), and there is no regular association.

REMARKS. Hummelinck (1936), Naumov (1960, 1969) and others listed by Calder (1970) regarded *Gonothyraea loveni* and *G. hyalina* as conspecific and I concur.

The distinctive method of reproduction has been described in part by many authors from Ellis onwards. Nevertheless *G. loveni* was widely confused with *Obelia* spp. and with *Laomedea flexuosa* until Wright (1858, 1859) realized it was distinct (Cornelius, 1977*a*; Cornelius & Garfath, 1980). But Wright did not provide a name. The species was soon named by Allman (1859*a*) who took Joshua Alder's suggestion (in litt.) that the species was valid. Alder was perhaps unaware of Wright's publications. From the literature it would appear that Wright and Alder worked independently; but since both communicated freely with Hincks (e.g. 1868 : preface) they could have been in touch directly. It may be difficult to find out who among these British workers really was first to recognize *G. loveni.*

Most of the life cycle is well understood and has been redescribed in detail by Miller (1973; see also Bergh, 1879, Wulfert, 1902, and Goette, 1907). Aspects of stolon growth were described by Wyttenbach, Crowell & Suddith (1973).

Laomedea gracilis Sars, 1850, 1857, was based on a mixed type series and this has caused confusion. The material illustrated in 1857 was partly *G. loveni* (see synonmy) but predominantly *Clytia hemisphaerica* (see Stechow, 1923*a* : 111). The material resembling *C. hemisphaerica* in this series is here designated lectotype. Hence the species name *loveni* Allman, 1859*a*, remains available. In any case, the name *gracilis* is preoccupied. This and other problems relating to '*L. gracilis*' are considered under *C. hemisphaerica*, where a new name is introduced in place of *L. gracilis* (p. 78).

Obelia hyalina Clarke, 1879, has been referred to *Obelia dichotoma* (by Cornelius, 1975*a* : 266) and is not *G. hyalina* Hincks. Hence Billard's (1931*a*) record of '*Obelia hyalina* Clarke' from Mauritania refers to *O. dichotoma* and not *G. loveni.* This homonymy is discussed further under *O. dichotoma* (p. 119).

The affinities of *G. loveni* are discussed above (pp. 47–49).

Genus ***HARTLAUBELLA*** Poche, 1914

Sertularia, Campanularia, Obelia and *Laomedea* auct., part.
Obelaria Haeckel, 1879 : 172 (part).
Obelaria Hartlaub, 1897 : 488 (homonym).
Hartlaubella Poche, 1914 : 76.

TYPE SPECIES. *Sertularia gelatinosa* Pallas, 1766; by monotypy.

DIAGNOSIS. Erect, colonial Campanulariidae with polysiphonic stems and second order branching; hydrotheca pedicellate, with diaphragm and castellated rim, without spehrule; no medusa stage (see Remarks under *H. gelatinosa*).

REMARKS. The genus name *Obelaria* Haeckel, 1879, was proposed as a nom. gen. nov. for the hydroid stage of *Obelia*, of which name it is a junior synonym (Cornelius, 1975*a* : 254). Haeckel included *Sertularia gelatinosa* Pallas, 1766, in its scope. Confusion was caused later when Hartlaub (1897) independently coined the generic name *Obelaria* to apply to a gen. nov. comprising *Sertularia gelatinosa* alone. Although Hartlaub's name is a homonym of Haeckel's and cannot be used, Hartlaub's generic concept is accepted here. The next available name for the genus is *Hartlaubella* Poche, 1914, of which *gelatinosa* has always been the only member.

Hartlaubella gelatinosa (Pallas, 1766)
(Fig. 16)

Sertularia gelatinosa Pallas, 1766 : 116–117.
Campanularia flemingii Deshayes & Edwards, in Lamarck, 1836 : 133–134.
Laomedea gelatinosa: Couch, 1884 : 4–5, 39–40; Hincks, 1852 : 85–86; Da Cunha, 1944 : 65–66; Vervoort, 1946*a* : 300–303, fig. 133 (syn. *Campanularia flemingii* Deshayes & Edwards).
Obelia gelatinosa: Hincks, 1868 : 151–154, pl. 26, fig. 1; Naumov, 1960 : 268–269, figs 157–158; Naumov, 1969 : 290–291, figs 157–158.
Obelaria gelatinosa: Haeckel, 1879 : 172, 173, 176; Hartlaub, 1897 : 488–495 (non Haeckel); Nutting, 1915 : 88–90, pl. 24, figs 1–5.
Hartlaubella gelatinosa: Poche, 1914 : 76; Stechow, 1925 : 522; Stechow, 1927 : 309; Teissier, 1965 : 17; Calder, 1970 : 1543; Cornelius & Garfath, 1980 : 283.
Campanularia gelatinosa: Ralph, 1957 : 820, fig. 1b–f.

TYPE LOCALITY AND MATERIAL. Belgian coast (Pallas, 1766; Ralph, 1957); specimen not located.

MATERIAL EXAMINED. BMNH collection, about 50 specimens.

DESCRIPTION. Colony elongate; small colonies loosely conical, large colonies bushy, up to *c.* 200 mm; main stems straight or branched, polysiphonic. Final branches monosiphonic, arranged irregularly all round stem, ± dichotomous, flexuose; internodes usually curved but sometimes straight, length varied, 5–9 rings basally. Hydrothecae on ringed, slightly tapering pedicels, long-campanulate to cylindrical; rim often abraded even but initially castellate with notch of varied depth in centre of each blunt cusp; embayments rounded; diaphragm transverse. Hydranth with 22–28 tentacles, hypostome spherical. Propagation by stolons in spring. Gonotheca ♂ = ♀, axillary, inverted-conical, sides smooth to sinuous; aperture wide, distal, on short collar; ova (4–6) and embryos larger than usual in family; nuclei of blastomeres large, with unusually conspicuous chromosomes.
*Variation.*Internode length and curvature, angle of flexure of stem and length : breadth ratio of hydrotheca are all variable. The hydrothecal rim often abrades smooth.

DISPERSIVE STAGE. Planulae, developing within the gonotheca. Some authors have mistakenly reported a medusa stage.

REPRODUCTIVE SEASON. May–August in NW France (Teissier, 1965); July, 1934, Northumbria (H. O. Bull, in Evans, 1978).

DISTRIBUTION. Recorded from southern Scotland, Oslo Fjord, Danish waters and part of the Baltic south to the Mediterranean and Black Seas. The species is common in Dutch, Belgian, Irish, Welsh, English and N & W French waters (Vervoort, 1946*a*; Leloup, 1952; BMNH collection; Billard, 1927; Teissier, 1965).

Trustworthy Scottish records are few and there seems only one this century, although the species is still common in NW England: Tay Estuary (Fleming, 1820; Alexander, 1932); Shetlands, Berwick Bay and Solway Firth (Johnston, 1847); ?Dundee (BMNH 1851.7.25.227, specimen not located). Hincks (1868) repeated several of these records and Norman (1869) gave another Shetlands locality. Recent English records are numerous, northerly ones including Northumberland (Alexander, 1932) and Morecambe Bay (J. Clare, pers. comm. & BMNH 1970.8.28.6–10).

The species was recorded from 13 localities in Oslo Fjord by Christiansen (1972) but his statement that the species occurs north to Finmark is questionable, and Linko (1911) and Broch (1918) listed no records so far north. Neither also did Kramp (1929, 1938), who likewise considered the species absent from Iceland and the Faeroes. Naumov (1969) gave an Iceland record without further detail; but with greater precision stated the northern limit in the Baltic to be ‘Port Liepaja = Libava’, Latvia. Kramp (1935) listed several Danish records north to Frederikshavn, NE Denmark, and repeated Stechow’s (1927) record from Travemünde, near the southern limit of the Baltic Sea. Rasmussen (1973) reported the species from Siaelland Island, southern Denmark.

Mediterranean records are few. Naumov (1969) gave 'Black Sea, Mediterranean and Gibraltar'. Although Picard (1958*b* : 197) expressly excluded the species from the Mediterranean list Rossi (1950 : 205) had earlier recorded it from NW Italy, the Adriatic and Strait of Gibraltar. Linko (1911) listed Black Sea material.

The species is known from Portugal (Nobre, 1931; Da Cunha, 1944) but has yet to be recorded so far south as Morocco (Patriti, 1970).

HABITAT. Intertidal, particularly in pools and run-off from saltings, and shallow depths offshore. Often in estuaries and tolerant of reduced salinity at least to 6·2‰ (Vervoort, 1946*a*). Also tolerant of silt.

The lower depth limit is probably *c.* 15 m. A record from 30 m off the Scilly Isles was based on *Obelia bidentata* material (BMNH 1969.9.9.6; mentioned, Robins, 1969). Couch (1844) recorded material from beneath intertidal stones and on algae, but that under stones might have been *Laomedea neglecta* (*cf.* p. 107).

REMARKS. The nomenclatural history of this species is involved. The name *Sertularia gelatinosa* was first applied by Pallas (1766) to the 'Corallina confervoides, gelatinosa alba, geniculis crassiusculis, pellucidis' of Ray (1724 : 34, para. 7). However, Ellis (1755 : 20, p. 11, figs B, b) assigned bryozoan material to Ray's species, providing clear illustrations. Linnaeus (1758 : 812) included the descriptions of both Ray and Ellis in a single species to which he gave the new name *Sertularia spinosa.* This name is currently applied to a bryozoan species in the combination *Vesicularia spinosa* (Linnaeus, 1758), for example by Prenant & Bobin (1956). The bryozoan name *Sertularia sericea* Pallas, 1776 : 114, was a nom. nov. for *S. spinsoa* and is its junior objective synonym. Pallas elsewhere (1766 : 116–117) adequately described *gelatinosa.*

Fleming (1820) noted that Ray and Ellis each described a different species but referred Ray's description to *Obelia geniculata*, not to the present species. However, Pallas' account is clear and he contrasted *gelatinosa* with both *O. geniculata* and *O. dichotoma.* Also he noted the polysiphonic stem and cusped hydrothecal rim—both unusual in *Obelia.* Even so, it could be argued that Pallas had material of *Obelia bidentata* before him since that species superficially resembles *H. gelatinosa.* There is some evidence that *O. bidentata* did not then occur in European waters. Even if it did, Pallas might have overlooked the fine cusps on the hydrothecal rim which are a main distinction. But despite these small doubts it seems highly likely that Pallas' description indeed refers to the present species. Hincks (1868 : 152) himself commented that Pallas' description was 'admirable, and is the only one we possess which is not positively incorrect'; so the case is strong. Hincks summarized some of the additional taxonomic confusion surrounding the species between 1820 and 1868.

Campanularia flemingii Deshayes & Edwards, in Lamarck, 1836, was based on material of the present species described by Fleming (1820) from Scotland—although Deshayes & Edwards gave the type locality as coasts of England! Fleming had referred his material to *gelatinosa* but noted that it disagreed with Pallas' description in having even hydrothecal rims. Fleming thought Pallas might have mistaken tentacle tips for castellations on the rim, and assumed that *gelatinosa* always had an even rim. Deshayes & Edwards thought Pallas too careful to make this mistake and concluded that two species were involved, one with castellations and one without. Probably Fleming's material simply had hydrothecae in which the rims were worn smooth! Johnston (1838, 1847) realized the confusion and referred *flemingii* back to *gelatinosa.* He was followed by Bedot (1905) and Vervoort (1946*a*), and I concur. Gray (1848), however, gave *C. flemingii* specific rank, but did not cite material. Gray seems usually to have relied heavily on Johnston's work but on this occasion clearly did not. Possibly Edwards, who sometimes worked on the British Museum collections, persuaded him to accept the species.

Thaumantias leucostyla Will, 1844 : 73, pl. 2, figs 16–17, based on an *Obelia* medusa, was referred to the present species by Bedot (1912 : 328) without comment; but as *gelatinosa* has no medusa stage this must be wrong (see next paragraph). It would be difficult to identify the medusa beyond *Obelia* sp. from Will's description.

Several authors, including Hincks (1852, 1868), have stated that *H. gelatinosa* releases a medusa, which it does not (Cornelius, 1975*a* : 279). It could be that Hincks and the others saw medusa release from *Obelia bidentata*. But the first European records of that species date from the early 1900s; and it seems improbable that Hincks would have made such a mistake when identifying a hydroid. His comment that the branches of *gelatinosa* 'droop slightly' fits *bidentata*, but this is not conclusive. Another possible explanation of his apparent mistake is that he took the unusually large ova of *H. gelatinosa* for developing medusae.

Couch (1844) had much earlier given a correct (and posthumous) description of the life cycle, reporting planula development and release, and early development of the young colony. In addition he noted that the planulae were propelled by cilia. But his contemporaries were still muddled, and had Couch lived a little longer he might have corrected some of the ensuing confusion. Van Beneden (1843, 1844) reported medusa release in *H. gelatinosa* but his material was actually *Obelia dichotoma* (see Cornelius, 1975*a*; and 1977*a* for other references). Hincks (1852) also attributed a medusa to *gelatinosa*. Van Beneden's error of identification was later appreciated by Hincks, who referred Van Beneden's material to a synonym of *O. dichotoma*, namely *O. longissima* (Pallas, 1766). Similarly, the much later report by Godeaux (1941) that *gelatinosa* had a medusa was also based on *O. dichotoma* material. It might be relevant that Godeaux worked at the Van Beneden Institute! Then Leloup (1947), paralleling Hincks, referred Godeaux' material to *O. longissima*.

A convenient distinction between *O. bidentata* and *H. gelatinosa* is that in side view the branches of *bidentata* show a graceful sigmoid curvature lacking in *gelatinosa*.

The large chromosomes illustrated here recall in shape and size those of *Obelia* medusae, shown by Faulkner (1929).

Genus ***LAOMEDEA*** Lamouroux, 1812

Laomedea Lamouroux, 1812 : 184.
Campanularia Lamarck, 1816 : 112 (part).
Lomedea Pickering, in Dana, 1846 : 689 (lapsus pro *Laomedea*, see p. 78).
Campalaria Hartlaub, 1897 : 449.
Eucampanularia Broch, 1910 : 184 (part; see p. 52).
Eulaomedea Broch, 1910 : 189; Millard, 1975 : 223.
Cmpanularia Mulder & Trebilcock, 1914 : 11 (part; lapsus pro *Campanularia*).
Laomedea (*Paralaomedea*) Hummelinck, 1936 : 57; Vervoort, 1946*a* : 285.
Eulaomeda Rees & Thursfield, 1965 : 102 (lapsus pro *Eulaomedea*).

TYPE SPECIES. *Laomedea flexuosa* Alder, 1857 (proposed designation by Cornelius, 1981). Broch (1905 : 10) proposed '*Laomedea loveni* Allman, 1859*a*' as type species but *loveni* was not among the species originally included in the genus and is not eligible.

DIAGNOSIS. Colonial Campanulariidae with: polyp generation forming upright colonies; stolon branching but not anastomosing; hydrotheca pedicellate, lacking spherule; true diaphragm present; annular perisarc thickening inside base of hydrotheca; gonotheca stolonal or axillary, aperture typically circular, wide; gonophores sessile, interpreted as vestigial medusae in many species.

REMARKS. I have previously pointed out (Cornelius, 1975*a*) that *Laomedea* Lamouroux, 1812, is a junior synonym of *Obelia* Péron & Lesueur, 1810*a*. But the name *Laomedea* is so well known that I have submitted a case to the International Commission on Zoological Nomenclature recommending that it be conserved by application of the Plenary Powers. I have proposed that *Laomedea flexuosa* Alder, 1857, be designated type species although it was not originally included. The alternative, of applying the Rules of Nomenclature, would result in the virtually unused name *Campalaria* Hartlaub, 1897, being employed for the present genus. Further details of the case, and another concerning the genus name *Campanularia* (p. 51), have been presented elsewhere (Cornelius, 1981).

The subgenus name *Eulaomedea* Broch, 1910, type species *Laomedea flexuosa* Alder, 1857, by monotypy, is a junior synonym. Stechow (1923*a* : 95) referred *Eulaomedea* to *Laomedea* Lamouroux, 1812, and apart from subgeneric use by Splettstösser (1924), Hummelinck (1936) and Vervoort (1959) there seems to have been no further appearance of *Eulaomedea* in the literature until Rees & Thursfield (1965). These authors upgraded *Eulaomedea* to genus status, including within its scope '*E. angulata*', '*E. flexuosa*' and '*E. calceolifera*'. Finally Millard (1975) employed *Eulaomedea* to embrace *flexuosa* and *calceolifera* alone. Thus the name has not been widely used and Broch (e.g. 1918) himself came to drop it, without comment. For further details see Cornelius (1981).

The subgenus *Paralaomedea* was apparently introduced by Hummelinck (1936). The type species is *Laomedea neglecta* (Alder, 1856*b*; by monotypy). Vervoort (1946*a*) followed Hummelinck's usage. But the unusual acrocyst of *neglecta* was shown by Splettstösser (1924) to be medusoid in origin, so there seems inadequate reason for subgeneric separation.

Laomedea angulata Hincks, 1861*b*
(Fig. 17)

Laomedea angulata Hincks, 1861*b* : 261, pl. 8; Hummelinck, 1936 : 51–52, fig. 5; Picard, 1958*b* : 191 (syn. *L. sphaeroidea* Stechow); (*non* Da Cunha, 1944 : 63, fig. 36; = *Laomedea calceolifera*).

Campanularia angulata: Hincks, 1868 : 170–171, pl. 34, fig. 1, woodcut 14 (p. 136); Fraipont, 1880 : 433–466, pls 32–34; Billard, 1904*b* : 46, 47, 53, 55, 57, 65, 67, 72–82, 97, 144, 173, pl. 3, figs 1–7, pl. 5, figs 1–2, 7, 10; Faure, 1965 : 419–426, figs 1b, d, 2a, b, 3a, b.

Laomedea sphaeroidea Stechow, 1932 : 85–86.

Eulaomedea angulata: Rees & Thursfield, 1965 : 101–102.

TYPE LOCALITY AND MATERIAL. Hincks (1861*b*) based the original description on specimens from South Devon and the Isle of Man. Some of this material is preserved as follows: (i) Hancock Museum, Newcastle upon Tyne, infertile colony on single blade of *Zostera* L. (eel grass), in spirit, labelled '*Laomedea angulata*, Ramsey, Isle of Man. Revd T. Hincks' and, on a second label, '*Campanularia angulata* Hincks' (mentioned, Cornelius & Garfath, 1980); (ii) BMNH, several colonies on blades of *Zostera*, in spirit, in two tubes. One contains a single, wide blade of *Zostera* supporting an infertile colony of *C. angulata*; the other tube five *Zostera* blades, all much narrower than that in the first, each supporting one or more fertile colonies of *C. angulata*. The two tubes, in one jar, jointly bear the registered number 1899.5.1.149. In the bottom of the jar, detached from the tubes, were two faded labels written by Hincks: '*Campanularia angulata* Hincks, Isle of Man', and ' *Campanularia angulata* Hincks, Britain'. There seems no indication which label originally belonged to which tube. Although the narrow leaved *Zostera* resembles that in the Hancock Museum specimen, labelled Isle of Man, there is no further indication that the BMNH thin leaved specimen came from there too.

Probably all this material was identified by Hincks at some time, but whether he saw it before or after the date of publication of the first description is not clear. Hence, it is not possible to decide whether the specimens should be treated as syntypes or neotypes.

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Laomedea sphaeroidea* Stechow, 1932, fertile colonies taken from *Zostera*, Sète, S France, microslide preparations; Munich Zoological Museum.

OTHER MATERIAL EXAMINED. BMNH collection, *c.* 30 specimens from Britain and the Channel Islands and 13 microslide preparations from the Lagoon of Venice. Amsterdam Zoological Museum and Leiden Natural History Museum, Netherlands, *c.* 20 specimens.

DESCRIPTION. Mature colony comprising several erect, monosiphonic stems inserted at approximately regular intervals on an almost straight, little branched or unbranched, smooth hydrorhiza; recorded reliably only on eel grasses; stolons usually (Fraipont, 1880; Billard, 1904*b*) growing parallel with the leaf margins. Stems flexuose, internodes markedly straight (rarely, faintly curved), angle between them 90°–120°, length : breadth ratio variable; 1–*c.* 10 annuli basally in BMNH material. Late in season stems terminate in long, often curling

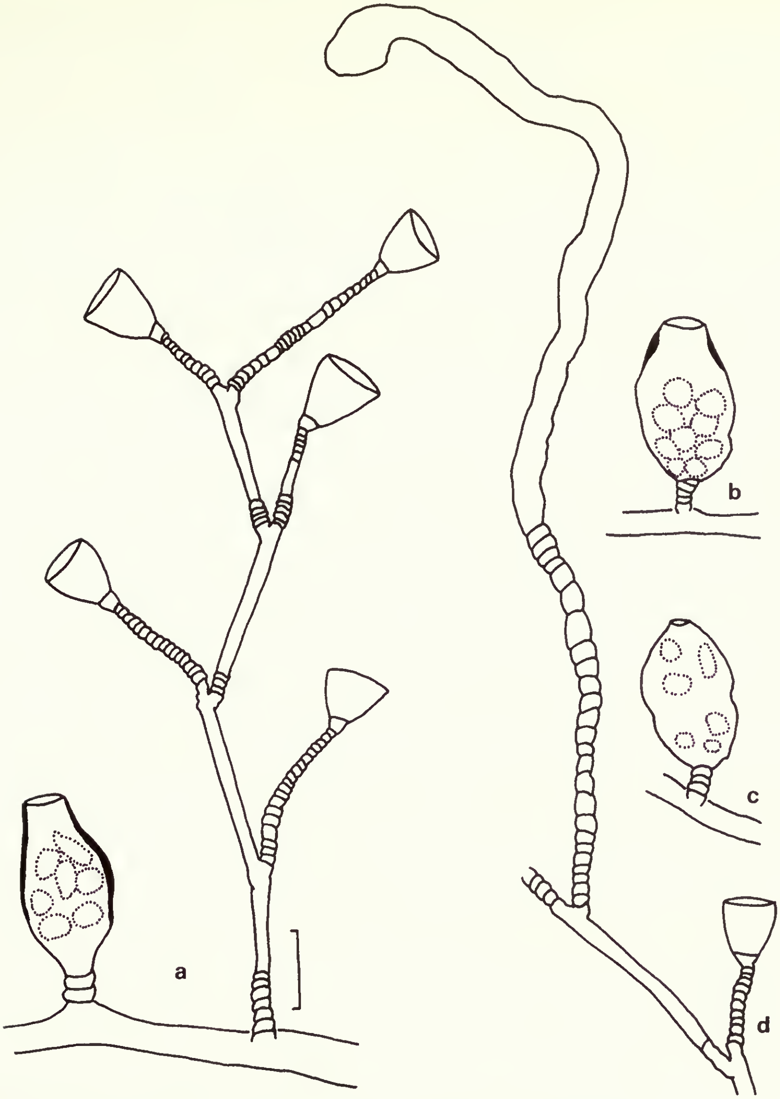


Fig. 17 *Laomedea angulata.* (a) part of colony, including hydrocaulus and stolonal ♀ gonotheca with embryos at different stages of development, Jersey; 1959.9.17.11. (b–c) ♂ gonothecae, Plymouth, SW England; 1959.9.17.3, 12. (d) vegetative terminal stolon; as (c). Scale (a–d) 500 μm.

tendrils approximately same width as internodes except at often recurved tip region which is wider. Tendrils probably represent modified hydranths: those of *Obelia dichotoma* differ (see Remarks). Hydrothecae campanulate, delicate, usually slightly flared distally, length *c.* 1½ times maximum breadth, thin walled and not thickened; diaphragm usually transverse but occasionally slightly oblique; pedicels 3–15 ringed, slightly tapering distally, sometimes with smooth central portion (e.g. BMNH 1959.9.17.11). Hydranth with 24–30 long tentacles alternately elevated and depressed; hypostome large, spherical when dead but (Fraipont, 1880) when alive constantly changing in shape; tissues colourless. Gonothecae apparently always borne on stolon. ♀ elongate-ovate, aperture distal, wide, on slightly demarcated neck, usually with sub-terminal internal strengthening ring; on short, 3–6 ringed pedicel; containing several eggs (see Remarks); planulae brooded internally. ♂ similar, aperture narrower;

containing several ♂ gonophores; sometimes said to be more tapered distally than ♀, but this not evident in BMNH series. No medusa stage.

Variation. Apparently minor. Broch (1933) regarded *L. calceolifera* a variety of the present species, proposing a forma *typica* for *L. angulata* s. str., but his opinion is no longer followed.

DISPERSIVE STAGE. Planulae, which develop within the gonotheca (e.g. BMNH 1959.9.17.11). Also vegetative tendrils which break away to form new colonies.

REPRODUCTIVE SEASON. Sexual reproduction June–August in NW France (Teissier, 1965), but fertile material recorded early as April in Isle of Man (Bruce *et al.*, 1963, material not examined). Vegetative reproduction involving tendrils typically August to November in NW France (Teissier, 1965).

DISTRIBUTION. A southerly species which probably occurs no further north than the British Isles. Unchecked published records and data with BMNH specimens indicate the following localities in NW Europe: SW Scotland (Rankin, 1901; Ritchie, 1911; Chumley, 1918); N & S Ireland (Hincks, 1868); Isle of Man (part of type series; also Bruce *et al.*, 1963); Scilly Isles, 1967 (Robins, 1969); S Devon, 1898 & 1906 (type series; also Marine Biological Association, 1957; a 1936 record on a barnacle seems unlikely); Dorset, BMNH; Roscoff (Fraipont, 1880; Faure, 1965; Teissier, 1965); Channel Islands (Vervoort, 1949; Leiden NHM & BMNH); Netherlands (Vervoort, 1946*a*; Leiden NHM). There seems only a single, unchecked record from the east coast of Britain, from St Andrews Bay (Crawford, 1895, repeated in Laverack & Blackler, 1974); and the species has not often been recorded from the many *Zostera* beds of southern England (see Addendum).

Published records from Spain southwards include the following: Santander, N Spain, (Rioja y Martín, 1906); NW Italy (Rossi, 1950; also Naples, Riedl, 1959, and lagoon of Venice, BMNH material); 'Mediterranean' (Picard, 1958*b*).

At Castiglione, Algeria, Picard (1955) found no less than 18 species of hydroids growing on the eel grass *Posidonia*, but did not report *L. angulata*. A single colony of the species was erroneously reported from Portugal by Da Cunha (1944), his illustration showing a mature ♀ gonotheca of *L. calceolifera*. The record from the Falkland Islands by James Ritchie, repeated by Rees & Thursfield (1965), was based on *Obelia dichotoma* material.

The northernmost material I have seen came from the Isle of Man (type series; also Bruce *et al.*, 1963). More northerly material was reported from the Clyde Sea by both Rankin (1901) and Ritchie (1911), the latter repeating some of Rankin's records and giving some new ones. However, the depth range given by the two authors, 30–130 m, exceeds the depths from which the species has otherwise been recorded. There are records of one of the substrate plants, *Zostera*, from the Clyde Sea area so it is conceivable Rankin and Ritchie at their deeper localities dredged up loose plants which had sunk; but dead *Zostera* often floats! Den Hartog (1970) gave 7 m as the deepest British record of *Zostera marina* L. (in the Scilly Isles) but cited Danish and Mediterranean records down to 11 m and one from the Pacific coast of the U.S.A. at 30 m, adding credibility to at least some of the Clyde Sea records. He gave the NE Atlantic distribution of *Z. marina* as Algeria (Castiglione), S France (rare) and N Mediterranean north to the arctic coast of the U.S.S.R., so it can be assumed that the northern limit of *L. angulata* is not determined by availability of eel grass.

However, the close association of this species with the eel grasses certainly affects its distribution. Thus *Zostera* almost died out in England in the 1930s (Tutin, 1942), and there is a virtual lack of *L. angulata* records since the 1900s. See also Addendum.

L. angulata was *not* recorded in several surveys of North Sea coasts, as follows: Northumberland and Durham (Robson, 1914), Norfolk (Hamond, 1957; Hamond & Williams, 1977), Belguim (Leloup, 1952), Denmark (Kramp, 1935; Rasmussen 1973) and W Sweden (Rees & Rowe, 1969). The record from Danish waters by Vervoort (1946*a*) probably referred to Broch's (1928) record as *Campanularia conferta* and should be rejected (W. Vervoort, pers. comm.). The species has still to be recorded from Denmark (K. W. Petersen, pers. comm.); but a record from the Great Belt, Kattegat, by Winther (1879, repeated in Stechow, 1927) if confirmed would be the most northerly of the species. A record dated 1960 from 20 m depth off SW Wales, quoted by Crothers (1966), seems dubious since both depth and area would be unusual. However, *Zostera* does occur there (K. Hiscock, pers. comm.).

HABITAT. Intertidal and shallow sublittoral, the deepest reliable record being 6–8 m (Studland Bay, Dorset, during or before 1890, coll. R. Kirkpatrick, pres. F. Beckford; BMNH 1899.7.22.1). Deeper records, from the Clyde Sea and off SW Wales, cannot be substantiated. Faure (1965) reported that *L. angulata* grew in a zone on the shore at Roscoff above that occupied by *L. calceolifera*; but the numerous records from shallow offshore localities show that *L. angulata* is not confined to the intertidal zone. A record from 64 fathoms (130 m) near the Falkland Is repeated by Rees & Thursfield (1965) was based on *Obelia dichotoma* material.

L. angulata has been widely recorded on the eel grasses, *Posidonia* and *Zostera* (Hincks, 1861*b*; Fraipont, 1880; Philbert, 1935*b*; Hummelinck, 1936; Vervoort, 1946*a*; Rossi, 1950; Riedl, 1959; Faure, 1965) and only seldom on other substances (sertularian hydroids by Bétencourt, 1888; *Laminaria* by R. Oppenheim, in Vervoort, 1949; *Dictyota dichotoma* by Philbert, 1935*b*; *Balanus improvisus* by W. J. Rees, in Marine Biological Association, 1957; *Fucus* by several recorders listed in Teissier, 1965). The overwhelming majority of published reports, and all the BMNH, Amsterdam Zoological Museum and Leiden Natural History Museum material are from *Zostera*, however, and it is likely that records on other substrates are wrong. Possibly some at least refer to *L. calceolifera*, since the two species were confused for several decades. Although Bétencourt noted terminal tendrils on his material it might have been *Obelia dichotoma* which also has tendrils and can look remarkably similar.

Nishihira (1968) made a detailed study of the hydroids epizoic on *Zostera* in northern Japan, but did not report *L. angulata* which seems (Stechow, 1923*b*) not to occur there. Picard (1955) made a similar study in Algeria, where he found *L. angulata* absent from the *Posidonia* beds of Castiglione.

The species is tolerant of brackish conditions. Hummelinck (1936) noted a tolerance of 9·8‰ Cl, a figure repeated by Vervoort 1946*a*) and, incorrectly as salinity, by Naumov (1960, 1969). The corresponding salinity figure is 17·7‰. Morri (1979*a*) found *L. angulata* in a range of salinities down to 27‰in Tuscany, Italy.

REMARKS. Athough Hincks (1868, 1871) and several subsequent authors distinguished correctly between the present species and *L. calceolifera* some later authors (e.g. Babič, 1912; Broch, 1928, 1933; Vervoort, 1946*a*; Naumov, 1960, 1969) regarded them conspecific. A summary of this confusion and a taxonomic assessment of the two species was provided by Faure (1965). The main differences are as follows, in approximate order from most to least useful. The gonothecae differ both in structure and position (hydrorhizal in *L. angulata*, on the stem and axillary in *L. calceolifera*). The internodes in *angulata* are usually straight, and curve slightly in most *calceolifera* specimens. Terminal tendrils are often present, particularly in autumn, in *angulata* but are unrecorded in *calceolifera* (*Obelia dichotoma* sometimes has them also). Eel grasses are probably the only substrate for *angulata* but *calceolifera* occurs on a variety of inert, solid substrates. Faure reported *angulata* growth at its peak in summer, and that of *calceolifera* in spring, at the same place. He reported erect stems spaced at 2–5 mm intervals in *angulata* and often clustered in *calceolifera*; but the extent to which this character in *angulata* is phenotypic, induced by the elongate shape of the eel grass leaves, is not known. Finally, Faure reported that colony height was 5–10 mm in *angulata*, 13–16 mm in *calceolifera*, each stem bearing respectively at maturity 4–6 and 10–15 hydrothecae. Despite this list of differences it remains difficult to identify some infertile material, even with the aid of long reference series; and some young colonies are probably impossible to identify.

A straight hydrorhiza occurs in *Obelia geniculata* also, in which it can be interpreted as a genotypic character adapted to keeping neighbouring, parallel-running hydrohizae adequately spaced along their whole lengths. *O. geniculata* occurs on broad thalloid algae, and spacing is probably an advantage. *L. angulata* is unusual among thecate hydroids in being closely adapted to its substrate in a number of obvious ways, and may have taken to living on eel grasses in relatively recent geological time. It seems likely that since eel grasses are themselves quite recent, being derived from more conventional terrestrial angiospermes, other campanularian and laomedean hydroids were living on algal substrates long before *L. angulata* or its ancestors took to eel grasses. Maybe hydroids of this group, having straight hydrorhizae, were pre-adapted to growing on the long narrow leaves of eel grasses.

However, at least some orientation of stolon growth occurs in *L. angulata* in a direction parallel with the eel grass leaf since diagonal or transverse stolons do not occur. *O. geniculata* stolons, although straight, are not orientated along the lamina and it may be that *angulata* stolon tips have a geotropic response which keeps them growing vertically (upwards or downwards) along the leaf, which floats upright when the tide is in. The fact that stolons of *angulata* grow sometimes along the narrow edges of the substrate leaves suggests that the planula does not seek a central position; or that once a tendril attaches and forms a new colony the hydrorhizal tip cannot locate the centre of the leaf; but there is no experimental evidence.

The terminal tendrils of *L. angulata* were found to be most common from August to November at Roscoff by Faure (1965). Billard (1904*b*) suggested that their function was to attach to adjacent eel grass leaves and hence enable the species to colonize fresh plants vegetatively. The tendrils of BMNH specimens differ from those of occasional *Obelia dichotoma* colonies in having dilated recurved end regions, the ends of *O. dichotoma* tendrils being uniform in width and approximately straight. Study of the BMNH material suggests that tendrils in *L. angulata* are modified hydranth/hydrotheca complexes.

The most detailed histological and general biological account of *L. angulata* is that of Fraipont (1880). However, he stated that the female gonophore contains a single egg; but one of his illustrations (pl. 34, fig. 3) showed a female gonotheca containing several planulae, as illustrated also here, and more than one egg seems normal.

The nominal species *Laomedea sphaeroidea* Stechow, 1932, was based on material from near Sète (Cette), S France, which Stechow (1919*a*) had earlier referred to *L. angulata*. The type material is referrable to *L. angulata* as defined here and it seems unnecessary to recognize the second species. Picard (1958*b* : 191) also suggested this synonymy, without comment.

Laomedea calceolifera (Hincks, 1871)
(Fig. 18)

?*Laomedea exigua* Sars, 1857 : 50–51.
Campanularia calceolifera Hincks, 1871 : 78–79, pl. 6; Faure, 1965 : 419–426, figs 1a, c, 2c, d, 3c, d; Miller, 1973 : 377–386, figs 6c, d, 10 a–d.
Campalaria conferta Hartlaub, 1897 : 495–496, pl. 19, figs 2–12.
Laomedea angulata: Babič, 1912 : 457–460, figs 1–5; Da Cunha, 1944 : 63, fig. 36.
Laomedea conferta: Splettstösser, 1924 : 403–420, figs X^1–Z^1, A^2–T^2; Da Cunha, 1944 : 63–64.
Laomedea calceolifera: Billard, 1931*b* : 390; Picard, 1955 : 187.
Obelia calceolifera: Picard, 1955 : 187.
Laomedea (*Campalaria*) *conferta:* Hamond, 1957 : 315, fig. 23.
Eulaomedea calceolifera: Rees & Thursfield, 1965 : 102; Millard, 1975 : 223–224, fig. 73g–k.

TYPE LOCALITY AND MATERIAL. Salcombe, Devon, England, 'on stones &c', offshore (Hincks, 1871 : 73–74, 79), several colonies in spirit and one microslide preparation; BMNH 1899.5.1.155. Some of the spirit material is attached to a worm tube, possibly a sabellariid (det. J. D. George).

TYPE MATERIAL OF OTHER SPECIES. Prof. Dr M. Dzwillo tells me that there is no material labelled '*Campalaria conferta* Hartlaub' in the Zoologisches Institut und Zoologisches Museum, University of Hamburg, where Hartlaub worked; and the type material is probably therefore lost. The original illustrations were detailed, however, and some appraisal of *Laomedea conferta* is possible.

I could not locate type material of *Laomedea exigua* Sars.

Other material examined. All BMNH non-type material is listed. Camara do Lobos, Madeira, 146 m ('80 fms'), coll. & pres. R. Kirkpatrick, ♀ colonies in spirit; 1922.3.4.6. 'Probably Woods Hole', Massachusetts, U.S.A., ex James Ritchie collection, parts of two colonies on microslide; 1964.8.7.83 (mentioned, Rees & Thursfield, 1965 : 102). Cape Town, Republic of South Africa, on moored raft, 15 Dec 1949, ♂ & ♀ colonies on two microslides; South African Museum coll. SH 423 (Fig. 18).

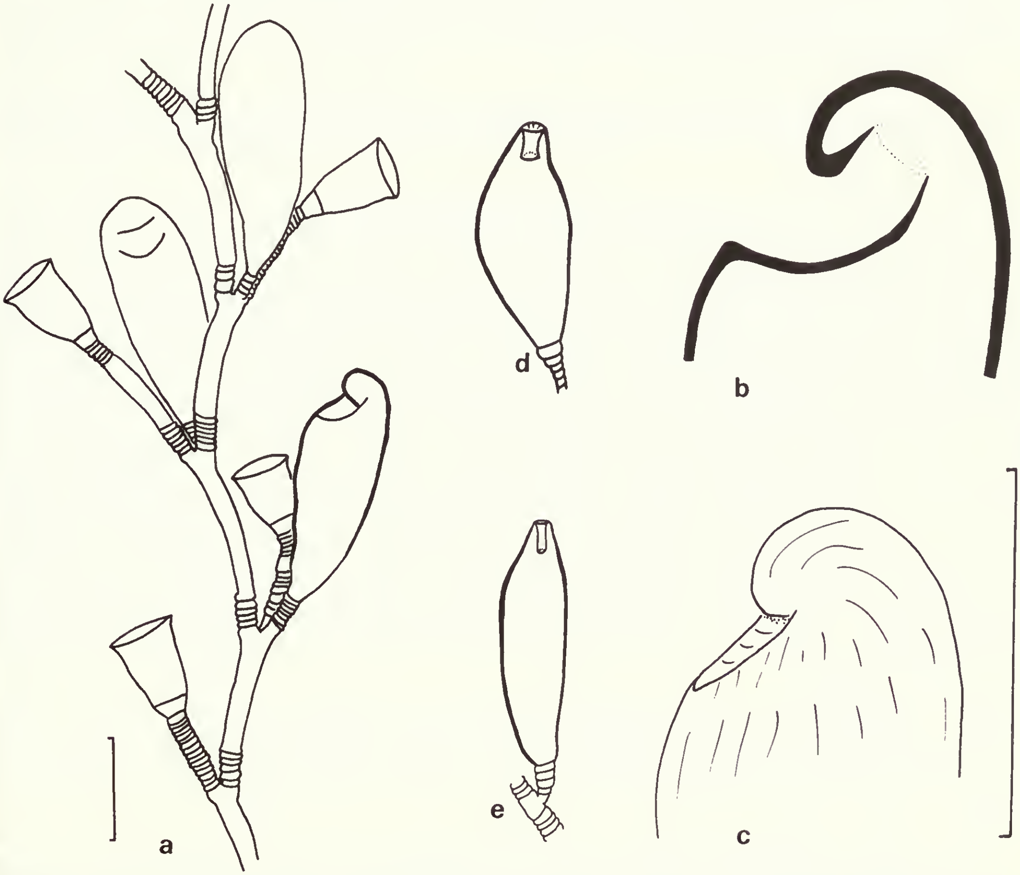


Fig. 18 *Laomedea calceolifera.* (a) part of ♀ colony, showing two mature gonothecae and, uppermost, an immature one. 'Probably Woods Hole', ex James Ritchie colln (mentioned, Rees & Thursfield, 1965 : 102); 1964.8.7.83. (b–c) optical sagittal section and sketch of part of lowermost gonotheca in (a). (d) ♂ gonotheca, Gulf of Pago, NW Yugoslavia; after Babič (1912). (e) ♂, Cape Town docks, ex South African Museum, microslide preparation SH423. Scale (a–c, e, and probably d) 500 μm.

Description. Mature colony comprising one to several erect, monosiphonic stems inserted at short, irregular intervals on a smooth, tortuous hydrorhiza. Stems probably usually unbranched, flexuose; internodes slightly curved to almost straight, long, 3–10 annulations basally. Terminal tendrils not recorded. Hydrothecae campanulate, delicate, flared distally, length *c.* $1\frac{1}{2}\times$ breadth, thin walled, rim even; diaphragm transverse to oblique; pedicels 3–20 ringed, sometimes with smooth central portion (Fig. 18). Hydranth (BMNH 1964.8.7.83) with 15–20 tentacles; hypostome large, probably sub-spherical in life. Gonothecae in axils, single or in clusters of up to 3; ♀ club-shaped with sub-terminal introverted curving tubular aperture on one side, several embryos developing internally; ♂ roughly cylindrical, elongate, tapering gradually below, more sharply above, aperture terminal, central, at end of introverted tube (as ♀ but straight). Young ♀ gonotheca truncate (Miller, 1973), lacking distinctive aperture until late in development (? young ♂ similar). Reproduction described in detail by Miller. No medusa stage.

Variation. Little information. Male gonothecae vary in width (Fig. 18).

Dispersive stage. Planulae, which develop within the gonotheca. Splettstösser (1924, as *C. conferta*) described the early stages in sporasac development and more recently Miller (1973) gave a detailed account of the whole reproductive cycle. Miller interpreted the sporosacs as retained medusae ('gonomedusae').

Reproductive season. Fertile material recorded April–August in NW France (Teissier, 1965), June off Norfolk (Hamond, 1957), December in the austral seasons of South Africa (present material).

Distribution. Widely distributed in warmer parts of the Atlantic Ocean, from South Africa (Millard, 1975) north to the English Channel and southern North Sea on the European coast and to Maine (Fraser, 1946) on the American side. However, published localities are few. For example the only definite British record since Hincks' description of the type material is from off Norfolk (Hamond, 1957, as *L. conferta*). Possibly the several British records of *L. exigua* Sars refer to this species: Swanage, Dorset (Hincks, 1868; possibly BMNH 1899.5.1.153 is this material); Kilve, N Somerset (Bassindale, 1941); and Great Yarmouth, Norfolk (Harmer, in Hamond, 1957). Other European records are as follows: R Rance and Roscoff, NW France (Philbert, 1935*b*; Faure, 1965; Teissier, 1965), Helgoland (Hartlaub, 1897, as *Campalaria conferta* and Portugal (Da Cunha, 1944, as *L. angulata* and *L. calceolifera*). The species has been recorded from the 'Mediterranean Sea' by several authors (Babič, 1912, as *L. angulata*; Billard, 1931*b*; Philbert, 1935*b*; Picard, 1958*b*) and, more precisely, from Castiglione, Algeria (Picard, 1955, as *Campanularia conferta*). Lastly Linko (1911) reported material from Sebastapol, Black Sea. Naumov (1969) stated that the species occurred along the 'Atlantic coast of England' and in the North Sea but he confused *calceolifera* with *angulata*, to which his notes may partly refer (see also Remarks concerning '*C. exigua*').

Habitat. Extreme lower shore (Faure, 1965) and shallow offshore (Hincks, 1871), sometimes deeper. Millard (1975) listed a record of an infertile colony from 70 m off South Africa; and one of the specimens listed above was said to come from 146 m ('80 fms') off Madeira.

Faure (1965) and Teissier (1965) recorded a usual substrate of rocks and pebbles. However, some authors (Hartlaub, 1897; Splettstösser, 1924; Vervoort, 1946*a*; all as '*conferta*') have noted an affinity for *Sabellaria* tubes (see also notes under Type material) while other 'living' substrates recorded include a spider crab (*Hyas araneus*) carapace and an ascidian (*Styela coriacea*) (both by Hamond, 1957, as *Laomedea conferta*), and intertidal *Lithothamnion* pools (Teissier, 1965). Morri (1979*a*, *b*) recorded *L. calceolifera* in a range of salinities down to 27‰ in brackish lagoons in Italy.

Remarks. For distinguishing features from *Laomedea angulata* see that species. Infertile specimens can be difficult to distinguish from some young, infertile *L. angulata* and *Obelia dichotoma* colonies.

Type material of the nominal species *Campalaria conferta* Hartlaub, 1897, could not be located but the original description and detailed illustrations agree with the type material of the present species in vegetative features. A difference, however, is that the material described by Hartlaub had gonothecae with truncated ends. Miller (1973) has shown that the peculiar asymmetric terminal region with its introverted tubular aperture forms late in ♀

gonotheca development, indicating that Hartlaub's account was probably of immature *L. calceolifera* material. Splettstösser (1924) and Hamond (1957) probably also had immature material which, following Hartlaub, they assigned to *C. conferta.*

The identity of *Laomedea exigua* Sars, 1857, remains obscure. The species was based on Gegenbaur's (1854) material from Sicily briefly described as *Campanularia* sp. nov. It might prove conspecific with *calceolifera*, which it predates. Van Beneden (1866), Hincks (1868) and Leloup (1947, 1952) assigned English Channel material to *exigua* but it seems likely their material was male *calceolifera.* Naumov (1960, 1969) provided a redescription of *L. exigua*, copying Hincks' figure of a colony and a gonotheca, already copied from Gegenbaur. He recorded the nominal species from the Black, Adriatic and Mediterranean Seas and the eastern North Atlantic from 'Gibraltar to the North Sea inclusive', but did not cite material. Probably his records refer to *calceolifera.* Bassindale's (1941) record from SW England might also have been young *L. calceolifera.*

Dimorphic gonothecae were probably first recognized in *L. calceolifera* by Babič (1912, as *L. angulata*), whose illustration of the male gonotheca is redrawn here.

Stolon growth was studied by Wyttenbach *et al.* (1973).

Laomedea flexuosa Alder, 1857
(Fig. 19)

Laomedea flexuosa Hincks, in Alder, 1856*b* : 440 (nom. nud.); Alder, 1857 : 122–123.
Campanularia flexuosa: Hincks, 1868 : 168–170, pl. 33.
non *Eulaomeda flexuosa:* Rees & Thursfield, 1965 : 102–103 (lapsus pro *Eulaomedea*; redet. *Obelia dichotoma*).

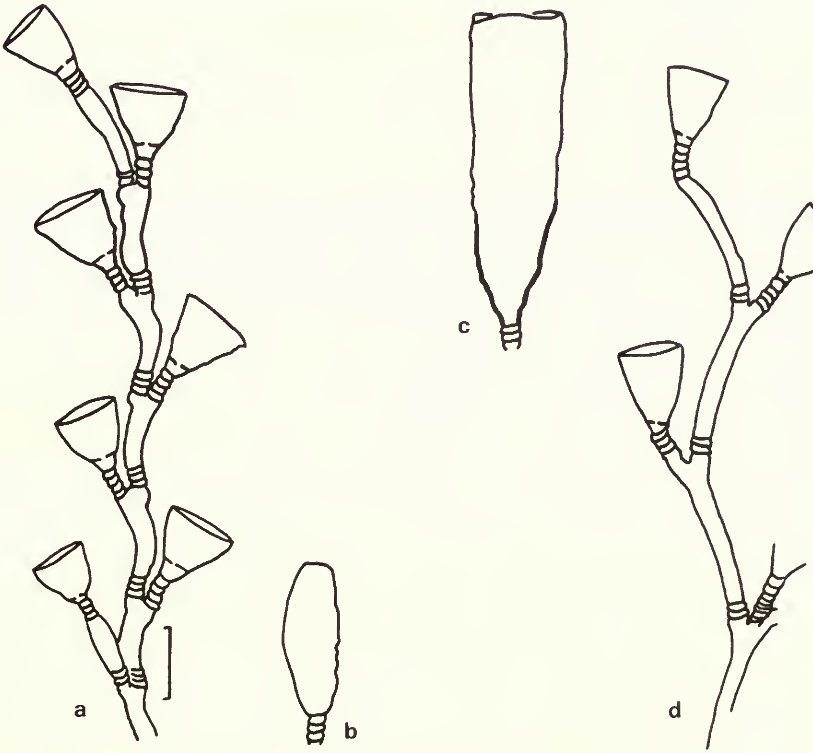


Fig. 19 *Laomedea flexuosa.* (a) New England, USA; 1915.3.6.7. (b) same, ♂ gonotheca. (c) ♀ gonotheca, ?British Isles: 1912.12.21.290a. (d) part of colony with internodes longer than normal, S Greenland; 1938.3.1.297. Scale (a–d) 500 μm.

NOMENCLATURE. The original publication of the name *flexuosa* (Hincks, in Alder, 1856*b*) lacked description, figures or other definitive indication but a description was published a year later (Alder, 1857). The species has been widely recognized and a lengthy synonymy is unnecessary.

TYPE MATERIAL AND LOCALITY. The type locality has been restricted to the British Isles by Cornelius & Garfath (1980). We listed the syntype material, which is preserved in the Hancock Museum, Newcastle upon Tyne.

OTHER MATERIAL EXAMINED. BMNH series, about 50 microslide preparations.

DESCRIPTION. Colony comprising often branched, erect stems up to *c.* 30 mm arising at irregular intervals from a straight, branching stolon. Stems and branches flexuose; internodes characteristically curved, length varied between colonies but constant within, each having 1–10 annuli basally. Hydrothecae campanulate, robust, sometimes asymmetrically thickened, length equal to or slightly longer than greatest width; rim even, diaphragm transverse; pedicels 3–20 ringed, slightly tapering distally, occasionally with smooth central portion. Hydranth with 17–23 tentacles, hypostome spherical. ♀ gonotheca subcylindrical, tapering basally, truncate distally; sides smooth to slightly sinuous; opening wide, terminal; pedicel short, ringed. ♂ shorter, tapering distally to narrower aperture than in ♀. Nematocysts described by Östman (1979). No medusa stage.
Variation. The following features are variable in the BMNH series: length : breadth ratio and radius of curvature of internodes (between, not within, colonies); length of hydrothecal pedicel and number of annuli; and gonothecal shape.

DISPERSIVE STAGE. Planulae, which develop within the gonotheca. Miller (1973) interpreted the gonophores as retained medusae ('gonomedusae'). Another description of their development was given by Goette (1907).

REPRODUCTIVE SEASON. Fertile material recorded April–July, Isle of Man (Bruce, 1948); June–July, 1934, Northumbria (H. O. Bull, in Evans, 1978); May–December, NW France (Teissier, 1965); February–March, May, September, S Spain (Chas Brinquez & Rodriguez Babio, 1977); November, Naples (Lo Bianco, 1909).

DISTRIBUTION. Recorded widely in the North Atlantic but status in some areas unclear. There are records from the Murman and White Sea coasts and Norway (intertidal pools, Mathiesen, 1928), the Faeroes and Iceland (Kramp, 1929, 1938), Hardanger Fjord, Norway (Brattegard, 1966) and the Shetlands southwards (Hincks, 1868; many other British authors). Records from warmer areas are numerous: Santander, N Spain (Rioja y Martín, 1906), S Spain (Chas Brinquez & Rodriguez Babio, 1977), Portugal (Da Cunha, 1950), Mauritania (Billard, 1906), Morocco (Patriti, 1970), Ghana (Buchanan, 1957); but not southern Africa (Millard, 1975). In the Mediterranean Sea the species has been recorded from Naples (Lo Bianco, 1909; Riedl, 1959) and 'E Adriatic' (Pieper, 1884).

The northern and southern limits on the North American coastline are also unclear. Although Kramp (1938) reported the species from W Greenland, Calder (1970) did not record it from Canadian waters and Fraser's (1944) most northerly record was from the Gulf of St Lawrence. The species has been reported along most of the United States coast, but the status in the Caribbean is just a single record which was doubted by both Fraser (1944) and Vervoort (1967).

HABITAT. Recorded on a wide variety of inert and living substrates (Hincks, 1868; Vervoort, 1946*a*; Marine Biological Association, 1957; Teissier, 1975; Chas Brinquez & Rodriguez Babio, 1977), probably lacking a strong substrate preference although often found on fucoid algae. Occurs intertidally, and probably not often deeper than the 37 m recorded by Miller (1961) and the 40 m from which a BMNH specimen was collected (reg. no. 1971.5.11.24, W Scotland). However, a deep record from '12 positions 20–48 miles (32–77 km) SW of Eddystone', SW England, 73–92 m (Marine Biological Association, 1957), suggests the species is not unusual at such depths; and Crawshay (1912) reported the species from

80–100 m at several stations in the western English Channel. The four microslide preparations listed under this species by Rees & Thursfield (1965), from depths down to 160 m, are of *Obelia dichotoma* material.

REMARKS. *Laomedea flexuosa* is type species of the unacceptable genus *Eulaomedea* Broch, 1910, and of the genus *Laomedea* (discussion of both on pp. 97–98).

Alder (1856*b*) introduced the name *flexuosa* in passing when describing *Laomedea neglecta* in the phrase '*L. flexuosa* Hincks, MS'; but the introduction was invalid as it lacked an acceptable indication. It is clear that in or shortly before 1856 Alder and Thomas Hincks concurred that *flexuosa* was a valid species, and were the earliest to recognize it. When first mentioning the name Alder (1856*b*) cited as indication 'the young of Johnston's small variety of *L. gelatinosa*'; but Johnston (1847 : 472) said that he had not seen material. He stated simply: 'variety α—with even margins and simple stem (not seen by me)'. Johnston apparently referred to hints by earlier authors that there was a species awaiting recognition. But Johnston did not see *flexuosa* material himself, nor did he cite this earlier literature. Hence Alder's (1856*b*) indication of Johnston's brief account does not satisfy the requirements of nomenclature, and the name *flexuosa* must date from the later paper (Alder, 1857).

The earlier mentions of the species which Johnston (1847) apparently had in mind are not easily traced. He may have thought that Couch (1844 : 39–40) had seen some *flexuosa* material when, in describing *gelatinosa*, he stated that species often to be just one inch (25·4 mm) high compared with the greater height usual in *gelatinosa* s. str. It can be noted that Couch might have included *neglecta* also within *gelatinosa*, since he recorded that '*gelatinosa*' sometimes grew under stones. Following Couch's early death it was left to Alder and Hincks to define correctly the three species involved. Thus, Alder (1856*b* : 440) stated that 'if observed [by earlier workers—possibly Couch] *neglecta* has been passed over as . . . *L. flexuosa*'.

L. flexuosa has been used by several experimental biologists. Stolon growth has been much studied and was mentioned above (p. 42). Phenotypic response to simple environmental changes was described by Crowell (1957; 1961; see p. 42). Embryonic rupture of the hydrothecal bud was studied by Knight (1965, 1970, 1971). Stebbing (1976, 1979) investigated the influence of inorganic toxins on growth, noting that sub-inhibitory doses actually enhanced growth rates. Factors such as straightness of stolon, growth rate and frequency of gonophore production were all affected by water quality. In a later paper (Stebbing, 1981) he studied several factors affecting growth.

The material assigned to this species by Rees & Thursfield (1965) I refer to *Obelia dichotoma.*

Laomedea neglecta Alder, 1856*b*

(Fig. 20)

Laomedea neglecta Alder, 1856*b* : 440, pl. 16, figs 1–2; Vervoort, 1946*a* : 308–310, fig. 316 (syn. *L. brochi* Splettstösser; *L. lauta* Hummelinck); (*non* Da Cunha, 1950 : 142–143, fig. 9).
Campanularia fragilis Hincks, 1863 : 46–47; Hincks, 1868 : 175–176, pl. 32, fig. 3 (syn. *C. elongata* Van Beneden).
Laomedea decipiens Wright, 1863 : 49, pl. 5, fig. 9.
Campanularia elongata Van Beneden, 1866 : 164–165, fig. 6 (p. 150); Leloup, 1947 : 24–25.
Campanularia neglecta: Hincks, 1868 : 171–172, pl. 30, fig. 2; Hincks, 1872 : 390–391, pl. 20, fig. 4.
Campanularia decipiens: Hincks, 1868 : 173–174.
Laomedea brochi Splettstösser, 1924 : 376–403, figs A–Z, A′–W′.
Laomedea ?lauta Hummelinck, 1930 : 35–37, fig. 5.
Laomedea (*Paralaomedea*) *neglecta:* Hummelinck, 1936 : 57 (syn. *?L. brochi* Splettstösser; *L. lauta* Hummelinck).

TYPE MATERIAL AND LOCALITY. Single infertile colony preserved as two microslide preparations, Hancock Museum, Newcastle upon Tyne, Northumberland; designated neotype by Cornelius & Garfath (1980). Although the neotype was once part of Alder's collections and was probably identified by him it almost certainly came from an Essex locality, whereas most of Alder's collections came from NE England. The type locality remains 'Cullercoats and Tynemouth, Northumberland, on undersides of stones' (designated by Nutting, 1915; repeated by Cornelius & Garfath).

TYPE MATERIAL OF OTHER SPECIES EXAMINED. *Laomedea lauta* Hummelinck, 1930, holotype; Rijksmuseum van Natuurlijke Historie, Leiden, reg. no. 259. Hummelinck's illustration of this material is very accurate.

OTHER MATERIAL EXAMINED (*L. neglecta* is only poorly represented in the BMNH collection). Porth Cressa, St Mary's, Isles of Scilly, on underside of block of granite, *c.* LWM, 17 Apr 1903, fertile colonies, 'ova in an external capsule' (ms note by E. T. Browne, Zoological Notebook **10** : 15, preserved in BMNH), spirit + 2 microslide preparations, coll. E. T. Browne; 1948.9.8.119 (Fig. 20). Mewstone Echinoderm Ground, near Plymouth, Devon, *c.* 50 m, October 1899, infertile colonies, coll. Marine Biological Association of the U.K., det. E. T. Browne (ms note in Zoological Notebook **13** : 149), spirit material (1948.10.1.126) + 1 microslide preparation (1959.9.17.19). Gåsö Ranna, Gullmarsfjord, Sweden, 20–30 m, 27 Aug 1962, infertile colonies, spirit material + 1 microslide preparation, coll. W. J. Rees; 1962.11.8.9. *Zooligisch Museum, Amsterdam:* Brehorn, Zuider Zee, Netherlands, 14 Jun 1927, infertile and ♂ fragments in spirit (Zuider Zee Onderzoek sta. 1; det. & mentioned Hummelinck, 1936 : 57, fig. 9 a–g) (Fig. 20). Dollard, NE Netherlands, fertile colony in spirit, coll. A. P. C. de Vos, 9 Aug 1954. Kornwenderland, NE Zuider Zee, 4–6 m, coll. Zoological Station, den Helder, 29 Sep 1938, several infertile fragments in spirit, det. W. Vervoort. *Rijksmuseum van Natuurlijke Historie, Leiden:* Aberystwyth Bay, Wales, 17 Jun 1939, intertidal, several infertile fragments, coll. P. W. Hummelinck; RMNH reg. no. 968. Strand Renesse, Schouwen, Netherlands, 20 Dec 1941, infertile fragments on *Tubularia ?indivisa* stems, coll. J. Viergever; RMNH reg. no. 702 (some of these specimens are polysiphonic, having two hydrocauli fused basally). Kornwenderland, 6 m, 29 Sep 1938, four small colonies on one microslide, coll. Zoological Station, den Helder, det. W. Vervoort; RMNH reg. no. 1012.

DESCRIPTION. A small species. Hydrorhiza smooth, tortuous, sometimes branched; short, delicate monosiphonic to bisiphonic stems arising at irregular intervals. Internodes long, narrow, often wider in middle than at ends, 3–10 rings basally, curved (recalling *L. flexuosa*) to almost straight (e.g. Hummelinck, 1936 : fig. 9a); each sharply inturned basally; hydrothecal pedicel on short distal process in line with axis of internode. Hydrotheca long, delicate, unthickened, cylindrical; length = 3 × width; diaphragm oblique to transverse; rim usually bimucronate but often abrades smooth; pedicel long, tapering distally, up to *c.* 20 annuli, sometimes with 1–3 smooth central portions. Hydranth with *c.* 20 tentacles (Van Beneden, 1866, as *C. elongata*; present material, 1971.5.11.11). Gonotheca (after Splettstösser, 1924, as *L. brochi*) ♂ = ♀, cylindrical to inverted-conical, truncated above. Acrocyst in ♀, eggs possibly extruded singly (Hincks, 1868; Splettstösser, 1924).

Variation. The delicate hydrothecal rim easily abrades smooth. Some published descriptions suggest that there are minute spines associated with the cusps on the hydrothecal rim but these seem simply to be folds. Splettstösser (1924 : fig. B, as *L. brochi*) illustrated a hydrotheca in which the bimucronate condition was obscure, and quite apart from damage by abrasion it seems that not all specimens are perfectly bimucronate. Other bimucronate species vary in the same way (*Obelia bidentata*, *Clytia paulensis*; see also p. 40).

DISPERSIVE STAGE. Planulae, brooded in ♀ acrocyst derived from vestigial retained medusa (Splettstösser, 1924). Developing eggs have been reported in the endoderm tissues of the stem (Splettstösser).

Hincks (1872) described what was apparently a vegetative spore developing in place of a hydranth, on a specimen collected from British waters in June.

Reproductive season. Probably April–October, but infertile colonies not unusual during this period. All available information is given: fertile material recorded Netherlands, 14 June, 1927 (Hummelinck, 1936; also present material) and 9 August, 1954 (present material); Isle of Man, August (Bruce *et al.*, 1963); Norfolk, England, 18 September, 1954 (Hamond, 1957); Northumbria, June (J. H. Robson, in Evans, 1978); SE Scotland, October (Laverack & Blackler, 1974); Scilly Isles, 27 April, 1903 (present material).

Infertile material recorded Netherlands, 27 August, 1929 (Hummelinck, 1936), 29 September, 1938 & 20 December, 1941 (present material); Aberystwyth, Wales, 17 June, 1939 (present material); Norfolk, 2 July, 1952 (Hamond, 1957); W Sweden, 27 August, 1962; SW England, October, 1899 (present material).

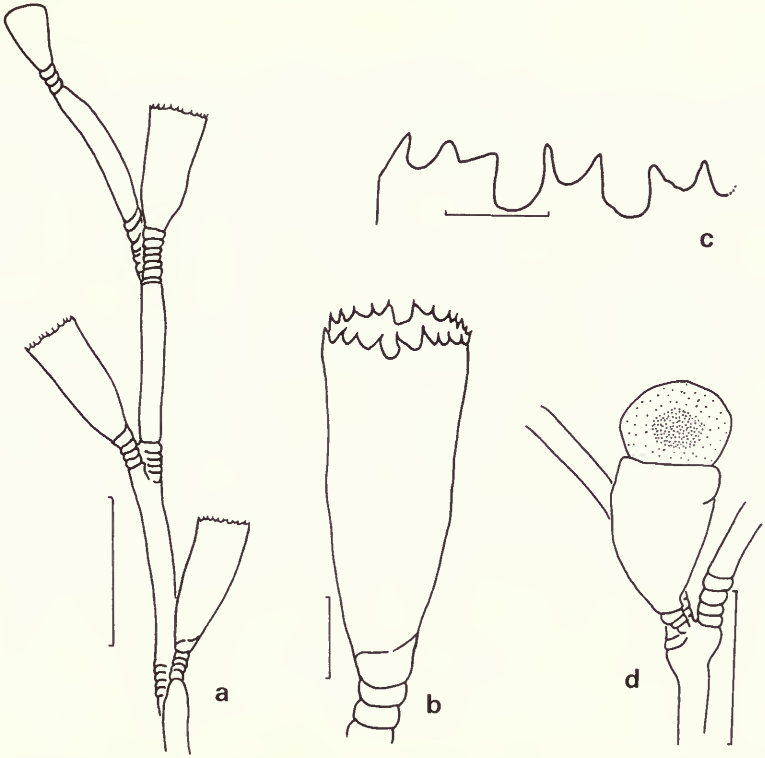


Fig. 20 *Laomedea neglecta.* (a) part of colony, Zuiderzee, Cl = 14·8‰; Amsterdam Zoological Museum collection. (b) same, one hydrotheca. (c) same, part of hydrothecal rim. (d) gonotheca with acrocyst, Is of Scilly, SW England; 1948.9.8.119. Scales: (a, c–d) 500 μm; (b) 100 μm.

Distribution. Although infrequently reported *L. neglecta* seems widely distributed in the North Atlantic. The most northerly and southerly records are from Iceland (Kramp, 1938) and the Adriatic Sea (Vatova, 1928). All other published records are listed (see also Material list): England (Alder, 1856*b*; Hincks, 1868, 1872; Hamond, 1957); Isle of Man (Herdman, in Wood, 1901 : 20; Bruce *et al.*, 1963, as *Campanularia fragilis*); Scilly Isles (Vallentin, in Browne & Vallentin, 1904; repeated in Robins, 1969); SE Scotland (Wright, 1859, as *Laomedea decipiens*, see Remarks; Laverack & Blackler, 1974); Aberystwyth, Wales (present material); Netherlands (Vervoort, 1946*a*); Belguim (as *C. fragilis*, Van Beneden, 1866, repeated in Leloup, 1947, 1952); Kattegat (Jägerskiöld, 1971; Rasmussen, 1973); W France (Billard, 1927).

Picard (1958*b*) did not include the species in the mediterranean faunal list but Vatova's (1928) adriatic record seems soundly based. The records by Broch (1933), from the Adriatic, and Da Cunha (1950), from Portugal, were probably based on *Obelia bidentata* material.

L. neglecta has also been recorded from the eastern coast of North America (Fraser, 1944).

HABITAT. Intertidal to at least 50 m. All available information is given: intertidal, underneath stones and on other hydroids (in Britain, Alder, 1856*b*; Hincks, 1868); under stones, on *Tubularia* stems and at 50 m depth (present material); 15–50 m on sea-beds of mud, clay and shell gravel (Kattegat, Jägerskiöld, 1971); 'on stone embedded in meshes of whelk pot', offshore, and under rocks in tidal creek (SE England, Hamond, 1957); on pebbles & oysters (W France, Billard, 1927); LWM, underside of rock (Scilly Isles, present material, Browne & Vallentin, 1904; repeated in Robins, 1969).

Collected in salinity of 26·7‰ from Zuider Zee (Hummelinck, 1936 : 57; data with specimen in Zoologisch Museum, Amsterdam).

REMARKS (see also Remarks under *Laomedea flexuosa*). *Laomedea neglecta* is a small species and although widespread has been little recorded. It was first described from English waters but there are still only a few records from Britain and Europe.

Infertile colonies resemble *Obelia bidentata*, and there is some overlap in hydrothecal length. Although the stems of *L. neglecta* are probably always narrower than those of *O. bidentata*, identification of small specimens can still be difficult.

The spines associated with the hydrothecal rim by several authors are merely folds in the hydrothecal wall appearing as artefacts during preservation.

Campanularia fragilis Hincks, 1863, was probably founded on a colony of the present species. The original illustration was actually published, without a binominal, a year earlier than the species name and description, in vol. 10 of the same journal, forming plate 9, figure 3. The illustration seems to represent *L. neglecta.* Hincks distinguished the two species on the 'markedly flexuose character of the stem', the long hydrotheca with plain rim and the small size of the colony. Probably the hydrothecal rims had abraded smooth. The holotype (not found) was collected from under stones in a rock pool, a likely habitat for *L. neglecta.* Hincks later (1868) referred to the species as *C. ?fragilis*, and significantly regarded *C. elongata* Van Beneden, 1866, type locality Ostend, Belgium, as conspecific. Vervoort (1946*a* : 310) quoted Maitland's (1897) opinion that *elongata* and *fragilis* were conspecific; an opinion Vervoort considered to have been a *pers. comm.* from Van Beneden to Maitland. Leloup (1947) concurred with this synonymy. There seems to have been no material recorded as *elongata* since the original description. Van Beneden illustrated a long hydrotheca with even rim and described the (infertile) colony as small. The hydranth had *c.* 20 tentacles. His description, like that of Hincks, probably represents *L. neglecta* with abraded hydrothecal rims.

Laomedea decipiens Wright, 1863, although described with some precision, was illustrated only by a small woodcut of a hydrotheca. Wright likened the species to *L. neglecta* except that the hydrothecal rim was 'even, and had the appearance of being double for about half its length from the rim', arguably a misinterpretation; and that 'the reproduction' of *L. decipiens* resembled 'exactly' the process he had described (Wright, 1859) in *Opercularella lacerata* (Johnston, 1847). That is, there was an external acrocyst. But Wright said his '*decipiens*' material differed in that each acrocyst contained only three ova, while those of *O. lacerata* had seven or eight. *L. neglecta* is now well known to have an acrocyst containing rather few ova. Further, its hydrothecal rims often wear smooth. Hence it is plausible that *decipiens* was based on fertile material of *neglecta* in when the hydrothecal rims had worn. Hincks (1868) repeated Wright's description and indicated that Wright had obtained his material from the Firth of Forth—Wright had given no locality. Wright and Hincks were in close contact (Hincks, 1868 : preface) and Wright probably told Hincks the locality. Hincks did not know the gonosome of *neglecta* and was rightly cautious when treating *decipiens.* The record from the Firth of Forth was repeated uncritically by Leslie & Herdman (1881) and Pennington (1885), but the species seems not to have been recognized since.

Laomedea brochi Splettstösser, 1924, and *Laomedea lauta* Hummelinck, 1930, were referred to the present species by Hummelinck (1936) and Vervoort (1946*a*) with good reason. See also the notes under Variation.

Da Cunha (1950) recorded *L. neglecta* from Portugal growing on a species of *Sertularella*. However, his illustration shows a medusa developing within a gonotheca and his material was probably *Obelia bidentata*.

The affinities of *L. neglecta* are discussed above (p. 47–49).

Laomedea pseudodichotoma Vervoort, 1959
(Fig. 21)

Laomedea (*Eulaomedea*) *pseudodichotoma* Vervoort, 1959 : 316–318, figs 56–57; Vervoort, 1966 : 104.

Type material and locality. Lectotype designated from original syntype series by Vervoort (1966), 50 mm ♂ colony with developing and mature gonothecae, 13° 43′ N, 17° 23′ W (off Senegal); mostly preserved in University Zoological Museum, Copenhagen, with part on microslide in Rijksmuseum van Natuurlijke Historie, Leiden. 'Paralectotypes', ♀ colonies, from 5° 37′ N, 0° 38′ E (off Ghana); also preserved in Copenhagen.

Other material examined. Off Abidjan, Ivory Coast, 35 m, 2 Mar 1966; Rijksmuseum van Natuurlijke Historie, Leiden, reg. no. 10410 (Fig. 21).

Description (partly after Vervoort, 1959, 1966). Colonies so far recorded up to 50 mm, polysiphonic basally; stem almost straight; roughly pinnate; some secondary branching; branches approximately alternate, in one plane, in the only available colony. Internodes slender, 2–3 ringed basally; some tanning. Hydrothecal pedicels short, 5–10 ringed; some axillary. Hydrothecae delicate, conical, some slightly swollen below; diaphragm oblique in side view, basal chamber large; rim even, circular. Gonothecae dimorphic. ♂ long, cylindrical to slightly tapering basally, widest about $\frac{1}{6}$ from aperture; truncate, aperture simple, not raised, as wide as gonotheca. Immature ♂ gonotheca much shorter. ♀ gonotheca long, widest in terminal $\frac{1}{4}$, tapering gradually below and abruptly above; truncate; aperture raised, half width of gonotheca; gonophores thought to be heteromedusoid, sessile.

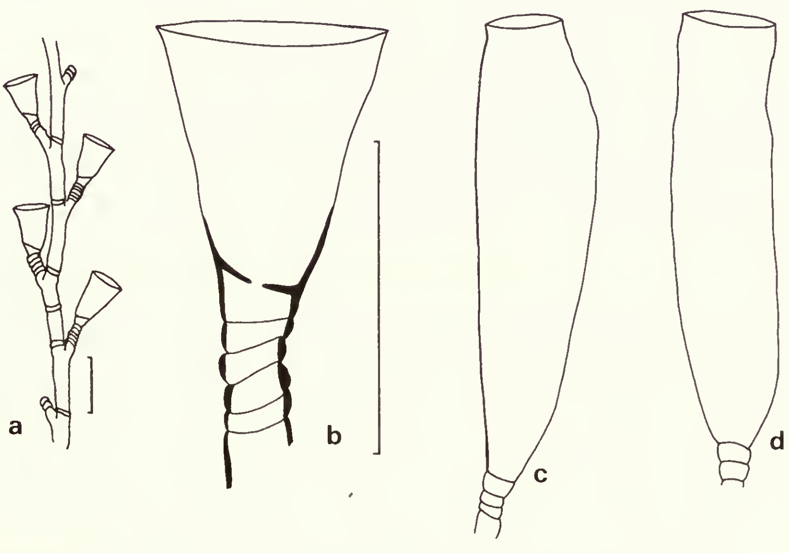


Fig. 21 *Laomedea pseudodichotoma.* (a–c) part of colony, single hydrotheca and ♀ gonotheca, Abidjan, Ivory Coast, 35 m. (d) ♂ gonotheca, off Senegal; syntype series. Scales: (a) 500 μm; (b–d) 500 μm.

DISPERSIVE STAGE. Almost certainly no medusa (Vervoort, 1959). Presumably planulae are released in the normal way.

REPRODUCTIVE SEASON. Fertile material recorded 30 January, 1946, 50 m, off Ghana, ♀; 2 March, 1966, 35 m, off Ivory Coast, ♀; 25 April, 1946, 65–89 m, off Senegal, ♂; (Vervoort, 1959; present material).

DISTRIBUTION. Recorded only from the coastal waters of Ghana, Ivory Coast and Senegal.

HABITAT. So far found only on *Sertularella cylindritheca* (Allman, 1888), at depths from 35 m to 89 m (Vervoort, 1959; present material).

REMARKS. This species is known only from tropical west Africa.

Genus ***OBELIA*** Péron & Lesueur, 1810*a*

Obelia Péron & Lesueur, 1810*a* : 355; Péron & Lesueur, ?1810*b* : 43.
Monopyxis Ehrenberg, 1834*a* : 297; Gray, 1848 : 84.
Obelomma Haeckel, 1879 : 176.
Obeliopsis Le Danois, 1913 : 110.
For other synonymy see Remarks, Cornelius (1975*a*) and page 114. See also note 3 (p. 124) concerning the date of introduction of the genus name *Obelia*.

TYPE SPECIES. *Obelia sphaerulina* Péron & Lesueur, 1810*a* (nom. nov. pro *Medusa marina* Slabber, 1769); by monotypy. For taxonomic purposes the type species was taken to be conspecific with hydroid *O. dichotoma* (Linnaeus, 1758) by van der Hoeven (1862 : 280) and Russell (1953 : 297), but this link is subjective. For the time being at least there is great difficulty in relating medusae collected from the plankton to their hydroids (e.g. Cornelius, 1975*a*). Péron & Lesueur cited as indication a specimen taken in Dutch waters, as illustrated in the German edition of Slabber's (1775–1781 : pl. 9, figs 5–8) work. But Goy (1980 : 72) links also to the published description an unpublished illustration by Lesueur. The specimen illustrated therein was taken near Le Havre, in the Museum of which town the illustration is preserved (see also note 3, p. 124).

Naumov (1960, 1969) and Stepanyants (1979) designated *Sertularia geniculata* Linnaeus, 1758, type species of *Obelia*; but *geniculata* was not an originally included species. For discussion see Cornelius (1975*a*, 1981).

DIAGNOSIS. Colonial Campanulariidae with: polyp generation forming upright colonies, branched or unbranched, variably flexuose; stolon not anastomosing; internodes annulated proximally, supporting hydrotheca on distal lateral process; hydrotheca bell shaped, hydranth with sub-spherical hypostome; gonotheca inverted cone-shaped, usually with raised terminal aperture but sometimes simply truncate; medusa umbrella flat, eversible, mesoglea thin; velum reduced to absent; manubrium long; about 16 marginal tentacles on release, numerous in adult, short.

REMARKS. An exhaustive synonymy and restriction of this genus have already been published (Cornelius, 1975*a*) but the most recent redefinitions of *Obelia* are by Stepanyants (1979) and Arai & Brinkmann-Voss (1980). The genera referred to *Obelia* by Cornelius included: *Slabberia* Oken, 1815 (a 'rejected work' for nomenclatural purposes); *Campanularia* Lamarck, 1816 (part; but see p. 51); *Thaumantias* Forbes, 1848 (part; see also p. 71); *Eucope* Gegenbaur, 1856 (part; here referred to *Clytia*, see p. 71); *Schizocladium* Allman, 1871; *Obelaria* Haeckel, 1879 (but see p. 94); *Obeletta* Haeckel, 1879; *Obelissa* Haeckel, 1879; and *Monosklera* von Lendenfeld, 1885. The nomenclatural problems involving *Obelia* with *Laomedea* are discussed above (p. 97).

Three species of *Obelia* are recognized from the hydroid stage in the eastern North Atlantic but their medusae cannot be told apart (Russell, 1953; Cornelius, 1975*a*; Arai & Brinckmann-Voss, 1980). Two of the species were described from the hydroid stage before any of the medusae, and their 'hydroid names' can be regarded as having safe seniority. The description of the third valid hydroid stage, *O. bidentata* Clarke, 1875, post-dates several binominals applied to the medusa stage and this name cannot yet be regarded safe. But there are difficulties in identifying to species level the early descriptions of the medusa and linking them with the correct hydroid stages. Thus it seems probable that the name *O. bidentata* will be unchallenged for some time, and that a working stability has been reached.

The subgenus *Monopyxis* was introduced in the combination *Sertularia* (*Monopyxis*) *geniculata* Linnaeus, 1758, by Ehrenberg (1834*a* : 297). *S. geniculata* is type species of the subgenus, by monotypy. Since there are only 3–5 species of *Obelia* recognized or provisionally accepted from the hydroid stage (e.g. Cornelius, 1975*a*) it seems superfluous to subdivide the genus, and *Monopyxis* can be referred to *Obelia*. Ehrenberg's account was based on material from Norway, Denmark and Germany. Gray (1848 : 84) used *Monopyxis* as a supergenus, including in it the species *Obelia geniculata, Hartlaubella gelatinosa, Campanularia flemingii* (now referred to *H. gelatinosa*, p. 96) and *Monotheca obliqua* (e.g. Hincks, 1868, as *Plumularia*); but this supergenus name was not employed again. Finally Hincks (1868) included *Monopyxis* in his synonymy of *Obelia*.

The genus *Obelomma* Haeckel, 1879, was established to include *Obelia* medusae with 48 tentacles on release. It included three nominal species, each incorporating several others within the synonymies Haeckel presented. Most of those incorporated are now referred to *Obelia*, of which *Obelomma* should be regarded a synonym.

The generic names *Obelaria* Haeckel and *Obelaria* Hartlaub are considered under *Hartlaubella* (p. 94); and *Eucope* Gegenbaur is treated under *Clytia* (p. 71).

The genus *Obeliopsis* Le Danois, 1913, was erected to include material referred to a single species (see p. 120) and can be confidently referred to *Obelia*.

General notes on the medusa stage and indications to other literature are given under *O. dichotoma* (p. 118) and in Cornelius (1975*a*). Applications of the genus name *Obelia* to bryozoan species were also listed in that paper.

The three species of *Obelia* (hydroid) occurring in the NE Atlantic can usually be identified from the characters given by Cornelius (1975*a* : table 1); but occasional specimens of *O. dichotoma* approach *O. geniculata* in having a slight thickening of the internodal perisarc. Some of these specimens cannot be confidently identified to species.

Obelia bidentata Clarke, 1875
(For illustrations see Cornelius, 1975*a*)

Obelia bicuspidata Clarke, 1875 : 58, pl. 9, fig. 1; Stepanyants, 1979 : 37–38, pl. 7, fig. 1 (syn. *O. austrogeorgiae* Jaderholm, 1904*a*; *Clytia paulensis* Vanhöffen, 1910).
Obelia bidentata Clarke, 1875 : 58–59, pl. 9, fig. 2; Jaderholm, 1904*b* : 270–271 (syn. *O. bicuspidata* Clarke; first reviser); Cornelius, 1975*a* : 260–265, fig. 2 (syn. *O. bicuspidata* Clarke).
Clytia arborescens: Billard, 1907 : 167 (*non* Pictet, 1893).
For further synonymy see Cornelius (1975*a*) and Table 4.

NOMENCLATURE. Jaderholm (1904*b*) acted as first reviser when using the specific name *bidentata* for this species, and several contemporary authors followed him (references in Cornelius, 1975*a*). Although the superseded name *bicuspidata* has been widely used, *O. bidentata* is the available name under the current conventions of zoological nomenclature.

DISPERSIVE STAGE. The medusa of this species has probably still to be reared to maturity but when young resembles those of the other two *Obelia* species (Cornelius, 1975*a*, 1977*a*). I did not mention in the 1975*a* paper that Professor K. Ramunni 'reared the medusa of this species' from Bengal material (mentioned in Annandale, 1915, as *O. spinulosa*). The age to which he reared it was not recorded. Ramunni was by far the earliest to realize that the medusa resembled that of the other two *Obelia* species, and to see it released.

DISTRIBUTION. Recorded from the English Channel and southern North Sea southwards through most European and African coastal waters but not from the Black Sea or the Baltic.

Table 4 Synonymies among the nominal species of *Obelia* described from the hydroid stage (after Cornelius 1975*a*, with additions). Although the lists are World-wide most of the nominal species have been recorded from the eastern North Atlantic. Many were first described in genera other than *Obelia*. Discussion of species treated in the 1975*a* paper is not duplicated here. The references cited in the table are mainly as in that paper, only the few additional ones being included in the present reference list.

(a) Synonyms of *Obelia bidentata* Clarke, 1875
O. bicuspidata Clarke, 1875
Campanularia spinulosa Bale, 1888
O. andersoni Hincks, 1889
O. bifurca Hincks, 1889
Gonothyraea longicyatha Thornely, 1899 (non *O. longicyatha* Allman, 1877)
O. corona Torrey, 1904
Obelia sp. Clarke, 1907
O. bifurcata Thornely, 1908
O. multidentata Fraser, 1914
O. oxydentata Stechow, 1914
O. longa Stechow, 1921
Clytia longitheca Hargitt, 1924
O. longitheca Hargitt, 1924 (sic)
O. attenuata Hargitt, 1924
Laomedea bicuspidata var. *picteti* Leloup, 1932
L. spinulosa var. *minor* Leloup, 1932
L. bicuspidata var. *tenuis* Vervoort, 1946
?*Clytia arborescens:* Billard, 1893 (see present paper, p. 117)

(b) Synonyms of *Obelia dichotoma* (Linnaeus, 1758)
Sertularia longissima Pallas, 1766
Sertolare genicolata Cavolini, 1785 (lapsus pro *Sertularia geniculata*)
?*Cymodocea simplex* Lamouroux, 1816
?*Tubularia clytioides* Lamouroux, in Freycinet, 1824
Campanularia maior Meyen, 1834
C. brasiliensis Meyen, 1834
C. cavolinii Deshayes & Edwards, 1836
C. caulini Chiaje, 1841
Laomedea gracilis Dana, 1846
O. commissuralis McCrady, 1857
L. divaricata McCrady, 1857
Eucope parasitica Agassiz, 1865
E. pyriformis Agassiz, 1865
E. articulata Agassiz, 1865
Campanularia flabellata Hincks, 1866
O. plicata Hincks, 1868
Schizocladium ramosum Allman, 1871
O. pygmaea Coughtrey, 1876
O. hyalina Clarke, 1879
O. adelungi Hartlaub, 1884
O. helgolandica Hartlaub, 1884
O. australis von Lendenfeld, 1885
C. cheloniae Allman, 1888
O. angulosa Bale, 1888
O. chinensis Marktanner-Turneretscher, 1890
O. arruensis Marktanner-Turneretscher, 1890
O. nigrocaulus Hilgendorf, 1898
O. gracilis Calkins, 1899

(b) Synonyms of *Obelia dichotoma* (Linnaeus, 1758) (continued)
O. surcularis Calkins, 1899
O. fragilis Calkins, 1899
O. griffini Calkins, 1899
O. rhunicola Billard, 1901
O. borealis Nutting, 1901
O. dubia Nutting, 1901
O. solowetzkiana Schydlowsky, 1902
C. obtusidens Jaderholm, 1905*a*
L. congdoni Hargitt, 1909
O. piriformis Bedot, 1910
O. pyriformis: Mayer, 1910
L. sargassi Broch, 1913
O. undotheca Stechow, 1923
O. nodosa Bale, 1924
O. coughtreyi Bale, 1924
O. obtusidentata Bedot, 1925
O. dischotoma Billard, 1927 (lapsus pro *dichotoma*)
O. everta Hargitt, 1927
?*O. commensuralis* Gudger, 1937 (?lapsus pro *commissuralis*)
O. alternata Fraser, 1938
O. equilateralis Fraser, 1938
O. microtheca Fraser, 1938
O. tenuis Fraser, 1938
O. racemosa Fraser, 1941
O. irregularis Fraser, 1943
O. braziliensis Vannucci Mendes, 1946
O. biserialis Fraser, 1948
O. hyaliana Vannucci, 1955 (see present paper, p. 119)

(c) Synonyms of *Obelia geniculata* (Linnaeus, 1758)
Laomedea lairii Lamouroux, 1821
Campanularia prolifera Meyen, 1834
Eucope diaphana L. Agassiz, 1862
E. alternata A. Agassiz, 1865 (nom. nov. pro *E. diaphana* L. Agassiz; non *Thaumantias diaphana* A. Agassiz)
E. polygena A. Agassiz, 1865
E. fusiformis A. Agassiz, 1865
O. gymnopthalma Spagnolini, 1871
Monosklera pusilla von Lendenfeld, 1885
O. geniculata vars *I, II & III* Marktanner-Turneretscher, 1890
Campanularia coruscans Schneider, 1897
O. geniculata f. *subsessilis* Jaderholm, 1950*b*
O. geniculata f. *gaussi* Vanhöffen, 1910
O. geniculata ff. *intermedia, subantarctica* & *subtropica* Ralph, 1956

There are few English records but from the north coast of France southwards there are many: NW France, Belgium, Netherlands (earliest records in Table 5; also Vervoort, 1946*a*; Leloup, 1947; Teissier, 1965); Cadiz, Gibraltar, Morocco, Mauritania, S of Madeira (Stechow, 1925); Algeria, Senegal (Picard, 1951*b*, 1955); Ghana (Buchanan, 1957); Gambia (Vervoort, 1959); Morocco (Patriti, 1970); Azores, Nigeria, Sierra Leone (Cornelius, 1975*a*); South Africa (Millard, 1975). The recorded northern limits are north of the Wash (Table 5) and Schiermonnikoog in the Frisian Islands (53° 30′ N, 6° 15′ E; RMNH Leiden, W. Vervoort, pers. comm.). By coincidence the most southerly records, from South Georgia and Tierra del Fuego (Cornelius, 1975*a*), are from a similar latitude, 54° S. A record from Adelie Land, Antarctica, may be based on *Clytia paulensis* material (see Remarks).

My statement (Cornelius, 1975*a*) that Kramp (1961) recorded the species from Helgoland was incorrect and there are no records from that island (W. Werner, pers. comm.) or from any other German waters. The Kent material which I listed was wrongly identified.

The Dutch record of Leloup (1933 : 11) listed in Table 5 was referred by Hummelinck (1936 : 56) and Vervoort (1946*a* : 300) to *Hartlaubella gelatinosa*; but Leloup also recorded *gelatinosa* in his paper. I have not located Leloup's material but if *O. bidentata* it would be among the earliest Dutch records.

Some aspects of the European distribution deserve comment. Although the species is distinctive and occurs widely in warmer parts of the Atlantic and Indo-Pacific oceans, it was not recorded from the eastern side of the Atlantic until the 1900s. It might previously have been confused with *H. gelatinosa*, as suggested by both Billard and Leloup in various publications. Confusion certainly occurred in some of the published records of the species from Belgium and England (possibly Leloup, 1933; Robins, 1969; both as *H. gelatinosa*; see previous paragraph and Table 5). Further, the species was poorly documented before 1900 and the descriptions available then were in obscure literature. It is understandable that when Billard (1902) recorded the first French material he referred it to *Obelia bifurca* Hincks, 1889, described from the Indian Ocean. (*O. bifurca* is now regarded conspecific.) Much later Stechow (1925) too referred material to *O. bifurca*, 50 years after *O. bidentata* had first been described; and it is evident that news of *bidentata* had spread slowly.

Although the European records (Table 5) appear to show the arrival of the species in Cherbourg and Ostend in 1902, the Netherlands in 1926, Norfolk in 1951, the Scilly Isles in 1966 and Hampshire in 1975 (an unusually hot summer), there is no satisfactory proof of a gradual extension of range. Indeed, the apparent spread of the species along the coasts of France, Belgium and the Netherlands follows quite closely the coming of hydroid experts in those countries, by coincidence from west to east (Billard, Leloup, Hummelinck, Vervoort). South-east England has seldom been given close attention by hydroid workers. Hamond (1957) recorded *O. bidentata* off Norfolk in 1951 as 'rather common' over a wide area, suggesting that it was already long established—but for how long cannot be decided. Parallel evidence comes from another overlooked species, similarly told from its near relatives by a bimucronate hydrothecal rim: *Clytia paulensis.* Although some BMNH material of *paulensis* was collected from near Plymouth in 1899 (p. 90) it was not identified for 80 years; and the species was first recognized from British waters independently in 1973. It seems that for a long time it too was overlooked and thought to occur no further north than NW France; but now it has been found again in southern England and, like *O. bidentata*, in East Anglia.

It remains puzzling that the nineteenth century English and Belgian experts active around the English Channel (Couch, Van Beneden, Gosse, Hincks) did not find *O. bidentata*. Hincks (1889) in fact described the species from Indian Ocean material, as *O. bifurca*, and would surely have recognized British examples. So it might really have been absent at that time; and it may be relevant that in 1937–1938 Vervoort (1946*b*) did not record the species from the Waddenzee, N Netherlands, where it now occurs. Finally, although *O. bidentata* has been recorded from the well worked offshore region around Roscoff (Billard, 1912; Teissier, 1965) it is scarce and has been found only in deep water (L. Cabioch, pers. comm.). See also page 44.

Table 5 Records of *Obelia bidentata* from the English Channel and southern North Sea. All known English records are included.

Locality	Date	Collector	Material	Literature	Comments
England					
North coast of Norfolk and the Wash, several localities	1951 on	R Hamond	BMNH 1953.11.16.1	Hamond, 1957	Earliest British record; probably most northerly of species to date; 53° 15′ N, 0° 45′ E
Darrity's Hole, Scilly Isles; 22–30 m	11 Jul 1966	University of London Sub-Aqua Club	BMNH 1969.9.9.6	Robins, 1969 (as *Laomedea gelatinosa*)	Earliest record for south coast of England
Hunstanton & Wells, Norfolk	22–23 Sep 1975; 13 Aug 1979	P F S Cornelius	BMNH 1975.10.10.7, 9; 1980.1.14.1	Unpublished	Live material from strandline
Langstone Harbour, Hampshire	Sep 1975	R G Withers	BMNH 1975.12.9.1	Unpublished	Small colony from moored raft
Netherlands					
Goes sluice, Zeeland	Aug 1926	?	RMNH, Leiden, 1174	Unpublished	Earliest Dutch record
Zuiderpier 'De Beer', nr Hoek van Holland	24 Aug 1928	?	RMNH, Leiden, 1172	Unpublished	
Kreupel, Zuiderzee; 52° 48′ N, 0° 20′ E; 3 m	19 Nov 1928	?		Hummelinck, 1936; Vervoort, 1946*a*	This locality since drained
Den Helder, North Holland	Jun 1933	E Leloup	?	Leloup, 1933	Doubted record; see Remarks
Renesse, Zeeland	pre-1946	P W Hummelinck	?	Vervoort, 1946*a*	Dead material from strandline
Renesse, Zeeland	20 Aug 1946	C J Verhey	BMNH 1976.11.12.1	Unpublished	
Belgium					
Blankenburge, nr Ostende	1902–1906, 1914	Various	?	Billard, 1922; Leloup, 1933	Earliest Belgian records
France					
St-Vaast-La-Hougue, Cherbourg	Probably 1902	A Billard	?	Billard, 1902	Earliest French record
Roscoff, 60–95 m	?1911 on	A Billard G Teissier	?	Billard, 1912; Teissier, 1965	Always scarce in Roscoff area (see text)

HABITAT. Substrates not recorded in my 1975*a* paper include an isopod, *Anilocra physodes* (Linnaeus), from Naples (Stechow, 1921*b*, 1925, as *Obelia bifurca*) and a commercial shrimp, *Pennaeus aztecus* Ives, from Florida (Kruse, 1959; via A. A. Fincham, pers. comm.); ships hulls, hermit crabs gastropod shells and algae (Millard, 1975). *O. bidentata* is highly tolerant of brackish water. It has been recorded at salinities of 18·6‰ (Netherlands; Vervoort, 1946*a*), 10–20‰ (Italy; Morri, 1979*b*) and even so low as 1‰ (S Carolina, U.S.A.; Calder, 1976). The species has often been recorded in shallow water and Millard (1978) listed it as intertidal.

REMARKS. A detailed, world-wide treatment has appeared recently (Cornelius, 1975*a*) and the notes given here are mainly intended to supplement that account. *O. bidentata* is a nearly cosmopolitan species, and a possible explanation is given above (pp. 44–45).

Differences from the superficially similar *Hartlaubella gelatinosa* are given under that species, and from the hydroid stages of other *Obelia* species by Cornelius (1975*a* : table 1).

Mayer (1910), Stechow (1925) and recently Stepanyants (1979) regarded *Obelia austrogeorgiae* Jaderholm, 1904*a*, as conspecific. I do not disagree (*cf.* Cornelius, 1975*a*) but have no fresh evidence. However, I cannot yet agree with Stepanyants that *Clytia paulensis* Vanhöffen, 1910, is identical with *O. bidentata.* The young medusae of both are sufficiently well described to indicate that two species are involved (see notes on Dispersive stage under the two species, pp. 89, 113). It could be argued that since Vanhöffen's material was infertile it was merely young *O. bidentata*: but this was not Stepanyants' argument. I believe neither Stepanyants nor I have seen the type material of *C. paulensis*. If it did prove to be young *O. bidentata* then a new name would have to be found for *C. paulensis* auct. (see synonymy in this paper). In that event it would be useful to apeal to the International Commission on Zoological Nomenclature to validate the widely used name *paulensis* sens. auct.

Clytia arborescens Pictet, 1893 : 34–35, pl. 2, figs 30–31, originally based on material from Indonesia, was reported south of Madeira at 100 m by Billard (1907); but Stechow (1925) included no further records in his synoptic list of warm water W Atlantic hydroids. Billard's material lacked gonothecae but, like the type material, had a compound stem and long hydrotheca (560–700 μm) with sharply pointed cusps. It is likely that his material was *O. bidentata*; and it is relevant that he had wrongly identified *O. bidentata* from the English Channel (see Distribution, above). *O. bidentata* was not well known at the time he published the *arborescens* record. The type material of *arborescens* was probably not *O. bidentata*, however, since Pictet reported hemispherical medusa buds in the gonotheca, indicating *Clytia* sp.

Obelia dichotoma (Linnaeus, 1758)

(For illustrations see Cornelius, 1975*a*)

Sertularia dichotoma Linnaeus, 1758 : 812.
?*Cymodocea simplex* Lamouroux, 1816 : 216, pl. 7, fig. 2 (see p. 121).
?*Tubularia clytioides* Lamouroux, in Freycinet, 1824 : 620, pl. 95, figs 6–8.
Lomedea gracilis C. Pickering, in Dana, 1846 : 689, pl. 61, figs 7, 7a–b (lapsus pro *Laomedea*; see p. 78).
Obelia dichotoma: Hincks, 1868 : 156–157, pl. 28; Cornelius, 1975*a* : 265–272, figs 3–4.
Obelia plicata Hincks, 1868 : 159, pl. 30, figs 1, 1a.
Campanularia cheloniae Allman, 1888 : 22, pl. 11, figs 2, 2a.
Obelia dischotoma Billard, 1927 : 332 (lapsus pro *dichotoma*).
?*Obelia commensuralis:* Gudger, 1937 : 1–6 (?lapsus pro *O. commissuralis* McCrady, 1857).
Obelia hyaliana Vannucci, 1955 : 56.
Laomedea plicata: Rasmussen, 1973 : 30, fig. 9.
Eulaomeda flexuosa: Rees & Thursfield, 1965 : 102–103 (lapsus pro *Eulaomedea*; redet.; see p. 105).
For further synonymy see Remarks, Table 4 and Cornelius (1975*a*).

DISPERSIVE STAGE. Medusae of *O. dichotoma* and *O. geniculata* reared from the hydroids in the laboratory still cannot be distinguished and some taxonomic confusion continues (Russell, 1953; Cornelius, 1975*a*; Arai & Brinckmann-Voss, 1980; see also Remarks). Russell's book includes the best account of the biology of *Obelia* spp. medusae.

The alternation of generations characteristic of medusoid coelenterates was actually first appreciated in scyphozoans, in 1829. It was reported in *Obelia* as early as 1836, first among the hydrozoans; but several still earlier workers had come close to its discovery in this genus. This and other historical aspects have been reviewed recently (Winsor, 1976; Cornelius, 1977*a, b*). A paper by Desor (1849) was missed by these reviewers. Desor provided an early confirmation of medusa release in *Obelia*, probably *O. dichotoma*. However, like several contemporary workers (see p. 97) he assigned his material to *Hartlaubella gelatinosa* which has no medusa. He probably identified his material using the well illustrated work of van Beneden (1844), who made the same error. Several other workers have assigned an *Obelia*-like medusa to *H. gelatinosa* and, despite the early clarification by Couch (1844), there was confusion for many years between *O. dichotoma, O. geniculata, H. gelatinosa* and *Gonothyraea loveni* (see notes under *H. gelatinosa* (p. 97), and Cornelius, 1977*a*).

Couch (1844) was in addition the first to note medusa release in *Obelia geniculata* (p. 120). Other early records in that species were contributed by F. W. L. Thomas (*in* Johnston, 1847 : 467), Hincks (1852 : 85) and Gosse (1853 : 84–90, pl. 4).

Illustrations of the medusae of *O. dichotoma* were first provided by Baster (1762, pl. 5, fig. 7), but the earliest of *O. geniculata* appeared nearly a century later, in Gosse's (1853) book.

Naumov (1969, as *O. longissima*, here referred to *O. dichotoma*) reported that 'the medusae were apparently not liberated from' Black Sea populations. But the species of *Obelia* are exceptionally well documented and since there is no other report of medusa retention in the genus a repeat of the observations would be desirable.

REPRODUCTIVE SEASON. Medusae of *Obelia* spp. have been reported around the British Isles in all months but are commonest from 'spring to late autumn' (Russell, 1953). Fertile colonies were recorded on the coast of Egypt between 6 Sep and 4 Oct, 1933 (Billard, 1936).

DISTRIBUTION. Found throughout European and African coastal waters with the exception of the Black Sea, from which there are no confirmed records (but see last paragraph of Dispersive stage). The species is remarkable in being nearly cosmopolitan in coastal waters and is one of the most widely distributed of hydroids. Aspects of this are discussed on page 45; and a detailed summary of locality records has appeared elsewhere (Cornelius, 1975*a*).

HABITAT. Tolerance of 12‰ salinity recorded by Calder (1976) in S Carolina. Unusual substrates noted in the literature included a sponge and the fins of a shark (Couch, 1844 : XV, as 'the sea thread of Ellis'), a turtle (Allman, 1888, as *Campanularia cheloniae*), a crab (Rasmussen, 1973: the colony was thought to be feeding on débris in the exhalent current); on the parasitic copepod *Lernaeocera* on the gills of a cod (*Gadus*); and on the back and claws of an anomuran 'crab', *Lithodes maia* (in Evans, 1978). Probably the record by Gudger (1937), of '*Obelia commensuralis*' on the blueback herring (*Alosa aestivalis*), referred to this species; but his account suggested that the hydrorhizae entered the muscles of the fish and the identification is not certain.

REMARKS. A revision of this species has appeared recently (Cornelius, 1975*a*) and only additional notes are given here. Identification of the hydroid stage is discussed above (p. 113). Nematocysts were described by Östman (1979) and by others whom she cited.

Tubularia clytioides Lamouroux, in Freycinet, 1824, was based on live material collected from algae in the Azores. Probably it was *Obelia dichotoma*. Rees & White (1966) evidently thought *Silicularia gracilis* Meyen, 1834, also described from Azores material, to be conspecific but while the *clytioides* type specimen was an erect colony that of *gracilis* was reptant. Rees & White presented a muddled synonymy, referring to the 'species' (*clytioides* + *gracilis*) as *Orthopyxis clytioides* (Lamouroux); and including in its synonymy the entry '*Silicularia clytioides* Meyen, 1834', evidently a lapsus for '*S. gracilis* Meyen'. Nutting (1915) had made the same error fifty years earlier (p. 50).

The once widely recognized nominal species *O. commissuralis* McCrady, 1857, based on the hydroid stage, was referred to *O. dichotoma* first by Böhm (1878), and again by me (1975*a*). Böhm's paper has been overlooked; and I know of no other works giving this synonymy.

Obelia plicata Hincks, 1868, described from infertile hydroid material, type locality 'Shetland', was recently referred to the present species without comment (Cornelius, 1975*a*). I have not been able to locate type material. The species deserves close evaluation as it has been recognized by several authors (Marktanner-Turneretscher, 1890; Nutting, 1915, as *?O. plicata*; Billard, 1927; Kramp, 1935, as *Laomedea plicata*; Fraser, 1944; Teissier, 1965; Rasmussen, 1973) although not by Broch (1912*b*). *O. plicata* was said by Hincks to resemble *H. gelatinosa* in having compound stems but the hydrothecal rims were even, not castellated. The hydrotheca was said by Hincks 'very much [to] resemble in form that of *O. dichotoma*'. Gonothecae were first assigned to *O. plicata* by Marktanner-Turneretscher (1890) who said they were the same as those of *O. dichotoma*. Indeed, the two species seem conspecific. Some older colonies of *O. dichotoma* (e.g. BMNH 1948.9.8.14, Plymouth, 21 Apr 1899, coll. E. T. Browne) exhibit compound stems resulting from overgrowth of up to 10 young, pale stems along the older, thicker and darker ones. The specimen mentioned resembles closely the colony illustrated by Hincks as *O. plicta*, and synonymy seems justified. Godeaux (1941, as *H. gelatinosa*) described similar *O. dichotoma* material, from the North Sea; while Billard (1927) maintained *O. plicata* distinct on the basis of the original characters. Broch (1912*b*) alone raised doubts, but was non-committal.

The factors causing overgrowth in occasional *O. dichotoma* specimens are not known, most colonies being solitary. However, such overgrowth has been described in other hydroids and called 'auto-epizoism' (Millard, 1973). If an overgrown specimen results from second and subsequent planulae settling on the original colony then the whole should be regarded as an aggregation of colonies, and not as a single colony. The phenomenon is discussed above (p. 40).

Campanularia cheloniae Allman, 1888, was based on infertile material collected during the '*Challenger*' expedition from the back of a turtle; but the locality of the turtle was not recorded. The original description and what remains of the type series (BMNH 1888.11.13.15, small colony in spirit + microslide preparation) are probably *O. dichotoma*.

Laomedea sargassi Broch, 1913, was recorded from Ghana by Buchanan (1957 : 360). The name *sargassi* was a nom. nov. for *O. hyalina* Clarke, 1879, introduced just to prevent confusion with *Gonothyraea hyalina* auct., and is therefore inadmissible under the current conventions of nomenclature. Congdon (1907 : 468) described material from Bermuda as *O. hyalina*, but Hargitt (1909) gave that material specific status, as *Laomedea congdoni*. I have previously (Cornelius, 1975*a*) referred *O. hyalina* Clarke and *O. congdoni* (Hargitt) to *O. dichotoma*, but overlooked the nom. nov. *sargassi*. Recent examination of the type material of *O. congdoni* (U.S. nat. mus. cat. no. 42647, microslide preparation of infertile fragments) confirms that it too is simply *O. dichotoma*. *Obelia hyaliana* Vannucci, ? in *ms*, was a name given to some '*O. hyalina*' material which Vannucci (1955) later considered conspecific.

Obelia geniculata (Linnaeus, 1758)
(For illustrations see Cornelius, 1975*a*)

Sertularia geniculata Linnaeus, 1758 : 812.
Obelia geniculata: Hincks, 1868 : 149–151, pl. 25, fig. 1, 1a; Cornelius, 1975*a* : 272–278, figs 1, 5.
For further synonymy see Cornelius (1975*a*), Remarks and Table 4.

DISPERSIVE STAGE. A medusa. See Remarks and notes under *Obelia dichotoma*.

REPRODUCTIVE SEASON. Russell (1953) recorded the following in British waters: *Obelia* sp. medusae found nearly throughout year, especially 'spring to late autumn' (Russell); medusae released at Plymouth, March–November (Orton, 1920); some evidence of lunar periodicity in release times (Elmhirst, 1925).

In the Mediterranean, Lo Bianco (1909) recorded medusa release at Naples March–June and October–January.

DISTRIBUTION. An almost cosmopolitan shallow water species found nearly throughout the eastern North Altantic.

The species was not recorded from the Black Sea by Naumov (1969). He listed the species as absent from the Baltic as well but Stechow (1927) reported it from Stockholm. It was recorded from Iceland and the Faeroes but not from Spitzbergen by Kramp (1929), although already known from Jan Meyen Island (Broch, 1918). Calder (1970) among others recorded the species from W Greenland; but I (Cornelius, 1975*a*) misquoted him as including E Greenland in its distribution. I know of no records from E Greenland.

HABITAT [see also Geographical distribution (p. 45), the habitat notes under *O. dichotoma* and Cornelius, 1975*a*]. The species was collected from the fins of a spur-dog (*Squalus acanthias*) by Couch (1844), who deduced that planula settlement must be rapid. Other actively swimming animals on which *O. geniculata* has been recorded include a sea-horse (*Hippocampus guttulatus*, by Zirpolo, 1939, 1940) and parasitic copepods themselves on fish (*Lernaeocera* spp. on *Gadus* (cod), by Leloup, 1931*b*; on *Lernaeocera* on *Clupea* (herring), by Debouteville & Nunes, 1951, 1952; on *Dinemoura* on *Cetorhinus* (basking shark) by Debouteville & Nunes). Long distance travel on floating algae has also been recorded (Arnaud, Arnaud, Intès & Le Loeuff, 1976). Recorded at 100 m depth by Naumov (1960). However, some of these records on fish might have been of *O. dichotoma*.

REMARKS. A revision of this species has appeared elsewhere (Cornelius, 1975*a*) and the present account simply adds to that.

Couch (1844) gave some interesting details. He stated the number of tentacles of the hydranth to vary widely (11–29 on p. 2, 14–28 on p. 38). He described medusa bud development but not medusa release, which was not known till 1847 in this species (Cornelius, 1975*a*, 1977*a, b*; see also p. 118). He recorded a range of tissue colour in the hydroid from 'white to deep red'.

The nematocysts were described by Östman (1979) and by others whom she cited.

Campanularia vermicularis Van Beneden, 1866, was described without illustrations and identification has been thought impossible (Vervoort, 1946*a*; Leloup, 1947). The species was based on Belgian material. Van Beneden kept live colonies for three weeks. He described the species as being more robust than *O. geniculata*, and as having larger hydrothecae and more numerous annulations. It was collected off the brown alga, *Fucus vesiculosus* L. The hydranth was said to have as many as 40–44 tentacles, a character which might one day help to identify his material (*cf.* Couch's observations, immediately above). Meanwhile I follow Vervoort in treating the species here but not including it in the synonymy.

Obelia spp. indet.

1. Hydroids. *Obelia longicyatha* Allman (1877 : 10, pl. 7, figs 4–5) was recorded from 35° 42′ N, 8° 40′ W (Cap Spartel, Tangier) and the Gulf of Cadiz by Billard (1907 : 168, as *Clytia longicyatha*), but the identity of the species remains unclear. I have discussed it elsewhere (Cornelius, 1975*a* : 264). See also the note on *Campanularia vermicularis* Van Beneden, 1866 (immediately above).

2. Medusae. Some species from the eastern North Atlantic cannot be assigned to a hydroid. *Obelia adriatica* Neppi (1912 : 726–727, pl. 3, fig. 8, 8a) was described from Adriatic material; and *Obeliopsis fabredomergui* Le Danois (1913 : 110) was based on material from the Little Minch, NW Scotland. It seems most unlikely that either is valid. *O. plana* Sars (1835 : 28, pl. 5, fig. 13, as *Thaumantias*) was referred to *O. flabellata* hydroid by Bedot (1910 : 484) and some later authors, and hence would fall in the synonymy of *O. dichotoma.*

But there seems slim reason for this identification (*cf.* Cornelius, 1975*a* : 271, footnote). Other pre-1910 medusa names in this genus were listed by Bedot (1901–1925) and Mayer (1910), and are not repeated here. As explained above (p. 118) most cannot be confidently assigned to a hydroid stage and a new list would serve little purpose.

Taxa now referred to other families

A few genera and species recorded from the eastern North Atlantic are no longer referred to the Campanulariidae. As several have been included in this family in some standard works notes on them are given here to summarize the current opinions. The taxa are treated in date order.

1. The genus *Capsularia* Cuvier, 1797, was used by Gray (1848 : 85–87) to embrace several British species of Campanulariidae but should be regarded a junior synonym of *Coryne* Gaertner, in Pallas, 1774 (discussion in Cornelius, 1975*b* : 378).

2. *Sertularia fruticosa* Esper, ?1810 [pl. 34, figs 1–2 (see note 2, p. 124); also Hammer, in Esper, 1829 : 162–163 (syn. *Sertularia laxa* Lamarck, 1816 : 116; *Laomedea sauvagii* Lamouroux, 1816 : 206; both nom. nov. pro *S. fruticosa*)] was recorded from the Adriatic Sea by Marktanner-Turneretscher (1890 : 205) as *Campanularia fruticosa.* The species is now referred to the genus *Thyroscyphus* in the family Sertulariidae (e.g. Vervoort, 1967; Millard, 1975). It is otherwise unrecorded from the eastern North Atlantic and Marktanner-Turneretscher's record may well be wrong. However, *T. fruticosus* occurs in the Red Sea as far north as the Gulf of Suez (Vervoort, 1967).

The exact date of publication of the species name is unusually difficult to determine and the necessary bibliographic work on Esper's important multi-part book has apparently not been done. Precise dating would be useful as the plates were issued several at a time around 1810, and they carry binominals. They thus predate the posthumous text, edited by Hammer (Esper, 1829), from which this part of the work is often thought to date. The plates predate also several important European works on zoophytes [e.g. those by Lamarck (1816) and Lamouroux (1812, 1816, 1821; Lamouroux *et al.*, 1824)]. Esper's work is rare, and few of the original wrappers survive; but the information on an incomplete set of wrappers in the BMNH library gives hope that dating would be simple if a complete copy were located. See also section 7, below.

3. The genus *Cymodocea* Lamouroux, 1816 : 214, originally included two species, *C. simplex* and *C. ramosa*, both described as new. *C. simplex* was based on material from Great Yarmouth and 'Ireland', *C. ramosa* on fragments from the Antilles. Johnston (1838) commented on the genus and on the identities of the two species; and Gray (1848) dismissed them as 'doubtful species' at the end of the Campanulariidae. Lamouroux (1821) and Lamouroux *et al.* (1824) included additional species in the genus but these do not enter the present discussion. Billard (1909), who saw some of Lamouroux' original material, referred the two species to *Nemertesia antennina* (Linnaeus, 1758), family Plumulariidae. I designate *C. ramosa* type species of the genus *Cymodocea*, the name of which hence becomes a junior subjective synonym of *Nemertesia* Lamouroux, 1812. Billard was confident that the *C. ramosa* material he saw was type, but had doubts about that of *C. simplex.* His doubts are significant since in J. Fleming's opinion, quoted by Johnston (1838), the original illustrations of *C. simplex* might be identified as an *Obelia dichotoma* colony lacking hydrothecae. I concur with Fleming's opinion; and disagree with Johnston who thought *simplex* was a plumularid. If the illustration is actually of *O. dichotoma* then Billard's caution was justified and the specimen he saw was not type. Almost all the Lamouroux collections were destroyed during the liberation of Caen on 7 July, 1944, so the *C. simplex* material is no longer available (Redier, 1967). However, *C. simplex* is here provisionally referred to *O. dichotoma* (p. 117).

The species *Cymodocea comata* Lamouroux, 1821, was recorded from the coast of Devon by W. E. Leach (in Johnston, 1838); but the species was referred to *Nemertesia ramosa* (Lamarck, 1816) by Billard (1909), who saw type material.

4. *Campanularia intertexta* Couch, 1844 : 41–42, pl. 11, fig. 3, was based on material then in the Museum of the Royal Institution of Cornwall, Truro. The material almost certainly no longer exists (Curator, Roy. Inst. Cornwall, pers. comm.). Johnston (1847 : 109–110) repeated Couch's description verbatim but regarded the species as unsoundly based. Gray (1848 : 88) listed it without comment, incidentally assigning to it Shetland material of *Lafoea dumosa* (Fleming, 1820), BMNH reg. no. 1847.9.24.66. At the same time Gray proposed the new genus *Conchella* (?lapsus pro *Couchella*), of which *Campanularia intertexta* is type species by monotypy. Hincks (1868 : 220) thought the species might be *L. dumosa*, stating that Couch's description was inadequate for identification. Later Bedot (1905 : 157) referred *intertexta* to '*Coppinia arcta*', an invalid species accepted by several nineteenth century authors but merely based on the coppinia or reproductive branch of *L. dumosa.* Couch's illustration shows an unidentifiable campanularid hydroid, possibly *Orthopyxis integra*, growing on a coppinia of *L. dumosa.* Thus the type 'series' was mixed. The name *intertexta* is here restricted solely to the illustrated coppinia, which becomes lectotype. Hence *Campanularia intertexta* is to be regarded a junior synoym of *L. dumosa*; and the genus name *Conchella* a junior synonym of *Lafoea* Lamouroux, 1821. See also page 65.

5. *Campanularia lacerata* Johnston, 1847 : 111, pl. 28, fig. 3, is now known as *Opercularella lacerata* and referred to the Campanulinidae (e.g. Millard, 1975). The species has been referred to a variety of genera in the literature, including *Capsularia, Laomedea, Wrightia* and *Calycella* (references in Hincks, 1868).

6. *Laomedea obliqua* Johnston, 1847 : 106–107, pl. 28, fig. 1, based on British material, is today known as *Monotheca obliqua* and *Plumularia obliqua* by different authors and referred to the Plumulariidae (e.g. Millard, 1975).

7. *Campanularia fruticosa* Sars, 1850 : 138–139, is today referred to *Lafoea dumosa* (Fleming, 1820), in the Lafoeidae (e.g. Cornelius, 1975*b*). It has often been given full specific status, as *L. fruticosa.* See also section 2, above.

8. *Campanularia abietina* Sars, 1850 : 139, based on Norwegian material, has long been known as *Grammaria abietina* and assigned to the family Lafoeidae (e.g. Cornelius, 1975*b*).

9. *Campanularia parvula* Hincks, 1853 : 178, pl. 5a, was probably based on material of *Calycella syringa* (Linnaeus, 1767) lacking operculae. Several authors have referred the species to *Lafoea* Lamouroux, 1821, but this seems wrong (references and discussion in Cornelius, 1975*b*).

10. *Campanularia gracillima* Alder, 1856*a* : 361, pl. 14, figs 5–6, based on hydroid material from NE England, has frequently been referred to *Lafoea*, family Lafoeidae; but lately to the species *Lafoea dumosa* (Fleming, 1820) (e.g. Cornelius, 1975*b*; Cornelius & Garfath, 1980).

11. *Laomedea acuminata* Alder, 1856*b* : 441, pl. 16, figs 5–8, based on hydroid material from NE England, is the hydroid of an *Aequorea* sp. medusa, family Aequoreidae. The two species recognized from British waters from the medusa stage were described earlier so the name *acuminata* should be regarded provisional. Although the medusa generation of the two can be separated the respective hydroids are morphologically identical, so far as is known. Hence at present it cannot be decided to which of the 'medusa species' *acuminata* should rightly be referred (Russell, 1953).

12. The nominal species *Laomedea tenuis* Allman, 1859 : 367–368, was once known as *Leptoscyphus tenuis* (e.g. Hincks, 1868). It is currently regarded as a campanulinid, having

been provisionally referred to *Phialella quadrata* (Forbes, 1848) by Stechow (1923*a* : 129) and Rees (1939 : 441). Browne (1896 : 479) summarized the mistaken observations by Allman who assigned the medusa of one species to the hydroid of another. *Campanulina tenuis* Van Beneden, 1886 : 174, 176, pl. 13, is a different nominal species, provisionally referred to *Aequorea vitrina* Gosse, 1853, by Russell (1953). Bedot (1910) listed an earlier homonym of *C. tenuis.*

13. *Campanularia fastigiata* Alder, 1860 : 73–74, pl. 5, fig. 1, based on Scottish material, was known for some decades as *Stegopoma fastigiatum.* Edwards (1973) showed that *fastigiatum* was the hydroid stage of the medusa *Modeeria rotunda* (Quoy & Gaimard, 1827), the binominal of which takes priority. The species is assigned to the family Laodiceidae (e.g. Rees & Rowe, 1969; Edwards, 1973; see also Cornelius & Garfath, 1980).

14. *Campanularia humilis* Hincks, 1866 : 298, is now known as *Cuspidella humilis.* Its affinities are unclear but it was removed from the Campanulariidae long ago (discussion in Cornelius & Garfath, 1980).

15. *Clytia eucophora* Haeckel, 1879 : 168, was a combination applied to the hydroid stage of *Eucopium primordiale* Haeckel, 1879 : 168 (sic), from Corsica. As Mayer (1910 : 236) pointed out, the two names are objective synonyms with the same date of publication. Mayer, as first reviser, suppressed *eucophora* in favour of *primodiale*; but at the same time referred Haeckel's species to *Eucope picta* Keferstein & Ehlers, 1861. Although Kramp (1961) omitted to treat *E. picta* there is no doubt that it and the Haeckel species should be referred to the Phialellidae. Weismann (1883 : 158) introduced the combination *Clytia eucopophora*, a lapsus of Haeckel's spelling.

16. *Campanularia mutabilis* Ritchie, 1907 : 504, pl. 23, figs 3–5, based on Azores material, is now known as *Scandia mutabilis* and referred to the Lafoeidae (e.g. Millard, 1975).

17. *Campanularia divisa* was attributed by Bassindale (1941 : 148) to Todd (1906 : 137) whom he supposed to have reported material from Ilfracombe. Bassindale misread Todd's list, which included *Campanularia* species and *Tubularia indivisa.* The word '*indivisa*' was split between the two lines (*in/divisa*) and evidently read wrongly by Bassindale.

18. The genus *Hincksella* Billard, 1918 : 22, was considered by Totton (1930) and Ralph (1957) to be closely related to the Campanulariidae, but is now referred to the Syntheciidae (e.g. by Millard, 1975).

19. The genus *Billardia* Totton, 1930 : 150 (type species *B. novaezealandiae*, by original designation) was based on southern hemisphere material. Totton assigned *Billardia* to the Campanulariidae but the genus is similar to *Hincksella* and like it comes within the scope of the Syntheciidae sensu Millard (1975), in my opinion. Blanco (1967*b*) and Stepanyants (1979), however, retained *Billardia* in the Campanulariidae. Possibly a greater understanding of the reproductive structures will help. Totton suspected that the blastostyles of *Billardia* were produced in place of hydranths, within the hydrothecae, but said his material was inadequately preserved for him to be certain. If his suspicion were confirmed the Syntheciidae would be the correct family for *Billardia.*

Notes

1 (See p. 65). G. D. Westendorp (1813–1868) apparently produced only two works involving coelenterates (Westendorp, 1843, 1853). Both were on the zoophytes of the Belgian coast. The first was a straightforward taxonomic account including some new genera and species, among them *Clytia ryckholtii* (here referred to *Orthopyxis integra*). Probably none is valid. His second work, published in 1853, was remarkable in being illustrated by dried specimens mounted on sheets. It is rare but still important since one of the included species was described as new in the 1843 work, and the specimens used in illustration might be considered types. The 1853 work comprised a printed title page, a printed page giving a list of species and localities, and 32 hebarium sheets each bearing one species. There were 16 hydroids, 14 bryozoans and 2 sponges. Examples of the work were seen by Neviani (1903), Bedot (1910 : 200–201) and Billard (1914; also seen by Leloup, 1947 : 5); and another, imperfect copy has recently been found in the British Museum (Natural History) (Cornelius, unpublished *ms* in BMNH). I have not seen an intact copy.

Neviani listed the 32 species but *C. ryckholtii* was not among them. The copy described by Billard (1914), in Brussels (Mus. roy. Hist. nat.; *inv. no.* 3440), similarly does not have *C. ryckholtii*. The BMNH example also does not include that species. The copy evidently came to the (then) British Museum library about 1867. Certainly a collection of specimens corresponding with Neviani's list was purchased from Westendorp at that time, and was given the 32 zoological accession numbers 1867.5.4.22–24 and 1867.5.7.1–29. The specimens were curated each under its own species, and the printed species list was cut up to provide labels which were in most cases glued to the herbarium sheets. Much, perhaps all, of this material survives and is still curated under the various species; but I have not found the title page of this copy.

Only one type specimen of any group is included in this collection, that of the hydroid, *Plumularia macleodi* Westendorp, 1843 (BMNH reg. no. 1867.5.7.7). It can be considered a syntype of *P. macleodi*; and is in fact a specimen of *Kirchenpaueria pinnata* (Linnaeus, 1758). *P. macleodi* is thus a junior synonym of *K. pinnata*. Billard (1914), working on the corresponding Brussels syntype specimen, reached the same conclusion.

2 (See p. 121). Some evidence was presented by Sherborn (1922 : 1, entry under Esper; Sherborn, 1926 : 2528, entries under *fruticosa, Laomedea* and *fruticosa, Sertularia*) that at least some of the plates of Esper's (1829) '*Die Pflanzen-Thiere*' appeared before 1816, possibly around 1810. Since the plates bear binominals, and might predate the synoptic works of Lamouroux (1812 onwards) and Lamarck (1816 onwards), correct dating is important. However, it seems that bibliographers have not yet dated the plates and Sherborn's (1926) provisional date of 1810 for the plate of *Sertularia fruticosa* Esper is the best compromise. Certainly the plate of *fruticosa* predated the works of Lamarck (1816) and Lamouroux (1816), which referred to Esper's plate as being already published. Indeed, they proposed new names in place of *fruticosa*. The three volume Esper work was issued in parts, some after Esper's death in 1810; and the few copies I have seen have been collated with the undoubtedly earlier *Sertularia* plates intermingled with the text. But the partial set of wrappers with the BMNH copy gives much detailed information, and a full set might enable all the plates of this scarce work to be dated accurately.

3 (See p. 112). Dating of the two works here listed as Péron & Lesueur, 1810*a*, ?1810*b*, has caused confusion. A clarification is desirable since in them many genus names of medusae were introduced which are still used. The works comprised the earliest serious systematic treatment of medusae, and these authors finally disbanded the genus *Medusa* Linnaeus, 1758. The first of the two works was one of a series of journal papers written by the two authors, and comprised their taxonomic treatment of medusae. Several other papers in the series also dealt with marine animals but are not important here. They have been listed by Goy (1980). The second work (Péron & Lesueur, ?1810*b*), a book entitled *Histoire générale des méduses*, brought the series of papers together each forming a chapter of the book. The book version was repaginated from 1 on, and was presumably published after the series of papers (although it might conceivably have been issued in parts as the papers appeared).

The publication date of the taxonomic paper (Péron & Lesueur, 1810*a*) has been taken as 1809 by most authors and this date might be inferred from the title page of the volume of the journal in which it appeared. But there is good evidence that it did not appear until January, 1810 (Sherborn, 1914; 1929 : 4455, entry under *Obelia*; Cornelius, 1975*a*; Goy, 1980). The book, the *Histoire générale des méduses*, has been almost entirely overlooked. It was dated

1809 in the *British museum catalogue of printed books.* But J. Goy (pers. comm.) and I concur that the book version almost certainly would have followed the series of papers, and so would have appeared at least as late as 1810 (unless the book version were issued in parts).

Hence the many names introduced by Péron & Lesueur almost certainly date from the 1810*a* paper, published January, 1810. Apart from minor heading changes the book version (?1810*b*) was apparently printed from the same 'blocks' as the series of papers. For taxonomic purposes the two versions differ only in date.

The numerous plates that were to have accompanied the account of the medusae (Péron & Lesueur, 1810*a*) were prepared but not published immediately (*cf.* Cornelius, 1975*a* : 253, footnote; 1977*a* : 49, footnote). But most of the illustrations showing Péron & Lesueur's 'new' species were brought together in an extremely rare work usually attributed to Lesueur alone (Péron & Lesueur, ?1815). This work was cited by Haeckel (1879, in several of his synonymies, as the *Planches inédités*) and Totton (1965 : p. 45, pl. 8) among others but almost all twentieth century medusa workers have overlooked it. Fewer than half a dozen copies are known (Totton, 1965; Goy, 1980). Goy (1980) cited evidence from the *P.-v. Seanc. Acad. Sci. Paris, 1795–1831* (issue covering 14 August 1815) **5** : 532, that 1815 is the correct date; and not ?1811 as given in the *British museum catalogue of printed books* (**187** : 111) under Péron alone. She concluded that the bulk of the illustrations, showing most of the nominal species newly described by Péron & Lesueur (1810*a*), were copied and published by a variety of contemporary compilers in their own works and so made public. They included such famous names as de Blainville, Cuvier, Milne Edwards, Lamarck and Lesson (references in Goy, 1980). The original Lesueur drawings are preserved in the Museum at Le Havre.

Although the bulk of the rare work (Péron & Lesueur, ?1815) comprised illustrations of medusae exquisitely drawn by Lesueur, the title page leaves no doubt that the authorship should be ascribed jointly to Péron & Lesueur (Mrs A. Datta, pers. comm.). Péron had died in 1810 and it can be inferred that Lesueur wished him still to be senior author, as he had been of the lengthy text (Péron & Lesueur, 1810*a*, ?1810*b*) of the work.

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Addendum

On 15 August 1981 I found *Laomedea angulata* (p. 98) common on the eel grass bed at Studland, Dorset. The previous record from the British mainland was dated 1906; and from Dorset was 1890, also at Studland. Whether or not the species had disappeared from that locality in the meantime might be hard to tell. On 15 September 1981 I found the same species abundant on eel grass near Misery Point, R Yealm, near Plymouth. At this locality too the status of the species during the last several decades was unclear.

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A new species of free-living nematode from the Firth of Clyde, Scotland

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Introduction

A new species of free-living marine nematode, *Odontophoroides paramonhystera* is described from a fine sandy beach in the Firth of Clyde, Scotland. It is similar to *Odontophoroides monhystera* (Gerlach, 1953) from which it differs primarily in having a precloacal supplement. *Odontophoroides monhystera* sensu Hopper, 1968, is renamed *Odontophoroides hopperi* nom. nov.

Odontophoroides paramonhystera sp. nov.

Figs 1, 2, 3 & 4

Material studied. Eleven males and nine females, deposited at the British Museum (Natural History): Holotype – ♂$_{1}$, BM(NH)1981.6.42; Paratypes – ♂$_{2-11}$ BM(NH) 1981.6.43–50 & 1981.6.59–60, ♀$_{1-9}$ BM(NH)1981.6.51–57 & 1981.6.61–62. Also an 'en face' view of a juvenile was prepared, BM(NH)1981.6.58. In addition specimens of *O. monhystera,* collected by Dr S. Lorenzen (1973) and Drs G. Boucher & M. N. Helléouët (1977), were examined.

Locality. Low water spring mark, fine sandy beach, Scalpsie Bay, Isle of Bute, Scotland.

Measurements. See Table 1.

Description. Slender, colourless, worms. No pigment spots or ocelli seen in preserved specimens. Cuticle finely, transversely striated (Fig. 3a, b). Six papillae visible in 'en face' view (Fig. 1c, juvenile): whether R$_1$ or R$_2$ not clear. Four R$_3$ cephalic setae, about 1¼ head diameters long. Two fine subcephalic setae associated with the subventral R$_3$ cephalic setae in females; not observed in males. Six cervical setae present; two subdorsal and four subventral, posterior subventral cervical setae more posterior in males than females. Stout lateral setae at base of amphids; about 15 μm long, but difficult to measure accurately due to the angle at which they project. Somatic setae in four irregular rows; length variable, but often longer in oesophagus and anterior gut regions. Amphids prominent, shaped like the head of a looped Shepherd's crook, with cuticularized borders; wider in males. Corpus gelatum displaced in about half of the male specimens but none of the females. Buccal cavity large, conical, cuticularized, with a complex arrangement of teeth (Fig. 1c, d). Six teeth present, bifurcate with a minor projection growing out of the main tooth. The four sublateral teeth are large and heavily cuticularized. Lateral teeth reduced to flat plates. Teeth attached at base to heavily cuticularized anterior section of buccal cavity (Fig. 1d). Two subdorsal, cuticularized tooth-like projections present; no equivalent subventral structures. In some preserved specimens the mouth was open, partially everting the teeth. Oesophagus muscular, especially in region which surrounds posterior section of buccal cavity; bulbs absent. Excretory pore prominent, located opposite posterior half of buccal cavity. Cellular sac in close association with posterior of excretory cell (Fig. 2b); function unknown. Caudal glands present lying entirely posterior to the anus. Tail conical.

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Table 1 Measurements of *Odontophoroides paramonhystera* (in μm unless otherwise stated).

		Holotype ♂	Paratype ♂♂					Paratype ♀♀				
Character			Nos	Mean	Range	SD[1]	CV%[2]	Nos	Mean	Range	SD	CV%
Length (mm)		1·529	10	1·403	1·330–1·522	·05	4	9	1·351	1·189–1·479	·11	8
De Man ratios	a	65	10	56	53–59	2·07	4	9	46	40–51	4·00	9
	b	8	10	7	7–8	·36	5	9	7	7–8	·42	6
	c	12	10	11	10–13	·79	7	9	10	8–12	1·26	13
	V%							9	20	18–22	1·10	6
Head width		10	10	13	12–14	·73	6	9	13	11–15	1·29	10
Cephalic setae length		14	10	15	14–17	1·30	9	9	18	14–20	2·03	11
Subcephalic setae length		4	10	5	5–6	·52	10	9	6	5–8	1·35	21
Amphid distance from anterior		4	10	5	3–5	1·45	29	9	4	4–8	1·41	35
Amphid length		11	10	12	11–13	·95	8	9	12	10–14	1·47	12
Amphid width		7	10	7	6–9	·81	12	9	5	5–7	·58	12
Buccal cavity length		31	10	32	28–34	1·62	5	9	32	27–36	2·35	7
Buccal cavity width		6	10	7	6–8	·52	7	9	6	5–7	·90	15
Nerve ring to anterior		126	7	116	112–129	7·20	6	5	127	126–129	1·48	1
Oesophagus length		196	10	194	186–202	4·70	2	9	192	174–199	8·41	4
Excretory pore to anterior		19	10	22	20–24	1·10	5	9	20	14–25	3·80	4
Excretory cell to anterior		—	6	248	243–257	5·10	2	9	243	221–254	9·69	4
Maximum body width		24	10	25	23–26	1·10	4	9	30	27–33	2·04	7
Mid-body setae length		4	10	5	3–6	·94	19	9	5	4–7	·85	17
Vulva to anterior								9	272	242–289	13·72	5
Ovary to vulva								7	804	745–846	39·02	5
Anterior testis to cloaca		816	9	835	719–957	94·00	11					
Spicule length (arc)		35	10	35	29–40	3·30	9					
Supplement to cloaca		25	10	23	17–27	3·30	14					
Anal body diameter		23	10	22	19–25	1·70	8	9	23	20–25	1·57	7
Tail length		131	10	124	110–139	9	8	9	126	100–140	11·57	9

[1] SD = standard deviation. [2] CV% = coefficient of variation.

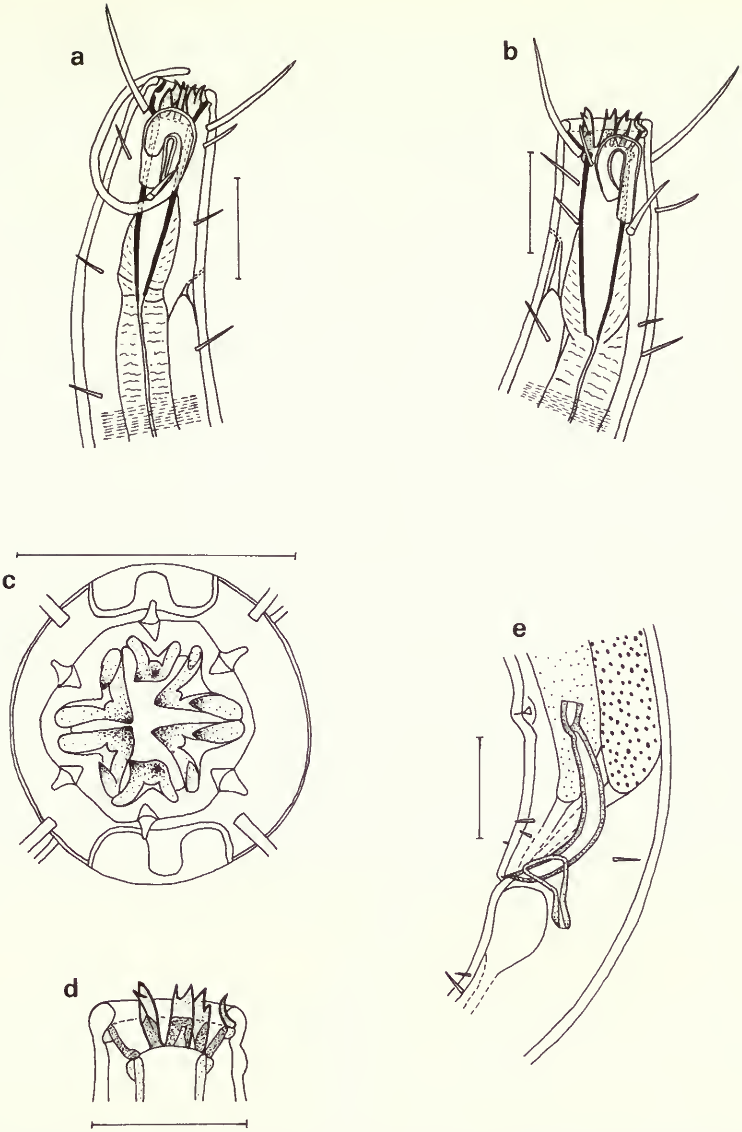

Fig. 1 (a) Head of male; (b) head of female; (c) 'en face' view of juvenile (dorsal is to the right of illustration); (d) teeth of female (dorsal is to the right of illustration); (e) cloacal region. Bar scale = 15 μm.

Male. Spicules paired, equal, arcuate, cephalate at proximal end slightly hooked at distal end; about $1\frac{1}{2}$ a.b.d. long. Gubernaculum appears to surround spicules and has narrow, paired, dorso-caudally directed apophyses. One supplement, with pore, 1 a.b.d. anterior to cloaca. Two testes, not clearly visible, outstretched, in tandem, ventral and apparently to left of gut; posterior testis about 250 μm behind anterior testis. Vas deferens widens into sac-like tube, of granular appearance, 4 a.b.d. anterior to cloaca.

Female. Vulva in anterior position. Vagina with cuticularized walls, surrounded by band of muscle, which is attached to ventral cuticle, the uterus, and to a tube-like structure. This tubed structure can give the false impression of connecting the sac associated with the excretory cell to the vagina (Fig. 2b). Muscle band presumably controls the opening of the

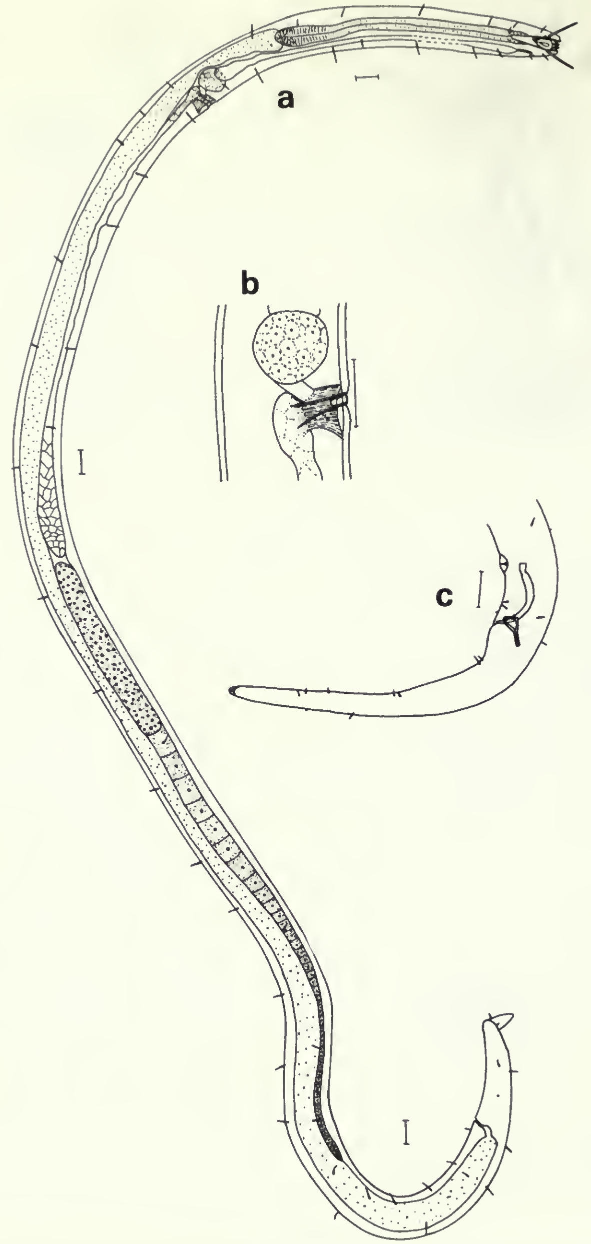

Fig. 2 (a) Whole female; (b) vulval region; (c) tail of male. Bar scale = 15 μm.

vulva. Single posterior ovary, outstretched, extending for most of the length of the body, ventral and to left of gut.

DIFFERENTIAL DIAGNOSIS. *Odontophoroides paramonhystera* sp. nov. is very similar to *O. monhystera* (Gerlach, 1953): the females and juveniles appear morphologically indistinguishable. However, males of the new species possess a precloacal supplement (lacking in *O. monhystera*) and the spicules are distally less slender.

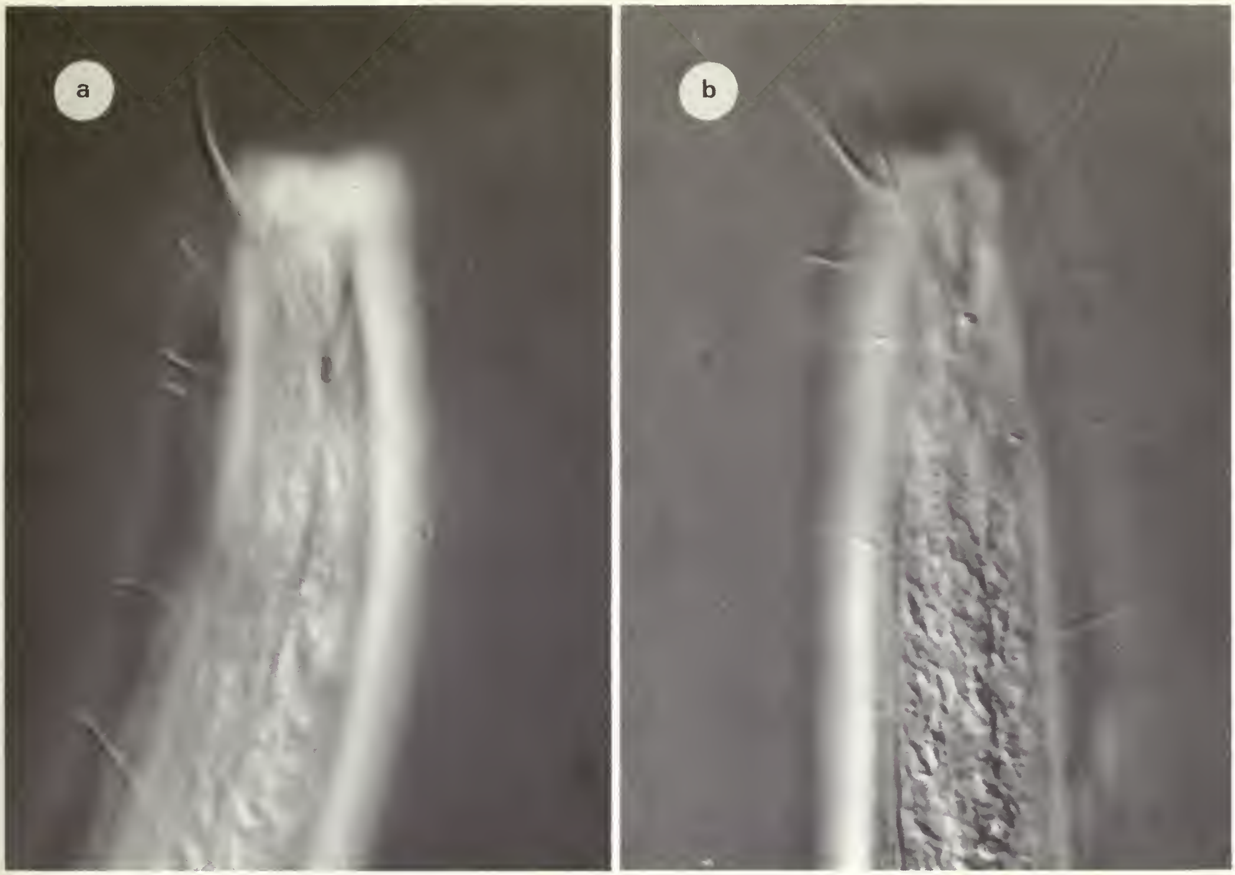

Fig. 3 Anterior of female, left lateral views: (a) showing amphid, cephalic and subcephalic setae, and lateral seta; (b) showing fine subcephalic seta associated with subventral R_3 seta.

Discussion

The previously monotypic genus *Odontophoroides* was erected by Boucher & Helléouët (1977) for *Synodontium monhystera* Gerlach, 1953. Gerlach (1953) originally described *S. monhystera* from Italy, and the types have been lost (Riemann, pers. comm.). However Gerlach (1953) noted 'Präanal-organe fehlen'. Subsequently a female was described by Hopper (1968) from Prince Edward Island, Canada, and males, females and juveniles described by Lorenzen (1973) from Helgoland, North Sea. Boucher & Helléouët (1977) also described a male (which has unfortunately been lost, Boucher pers. comm.), females and a juvenile from the English Channel. The type material of *S. monhystera* by implication, remains the specimens described by Gerlach (1953). Gerlach's (1953) and Boucher & Helléouët's (1977) descriptions show the distal ends of the spicules as less slender than Lorenzen's (1973) specimens. This character may, therefore, prove to be unreliable.

Odontophoroides monhystera sensu Hopper, 1968, is depicted without lateral subcephalic setae. The text refers to two lateral subcephalic setae, but notes them as positioned '8 μ and 23 μ, respectively, from anterior extremity' which would not seem to place them in their typical situation, i.e. at the base of the amphids. Lorenzen (1973) demonstrates that such setae are only present in adults and fourth stage larvae and Boucher (1974) shows the range of variation which may occur in the position of subcephalic setae in the related genus *Odontophora*, where species may or may not have lateral subcephalic setae. The presence or absence of these setae may therefore not be a stable generic character. In other respects Hopper's (1968) specimen is clearly *Odontophoroides*, being monodelphic (V = 19%) and

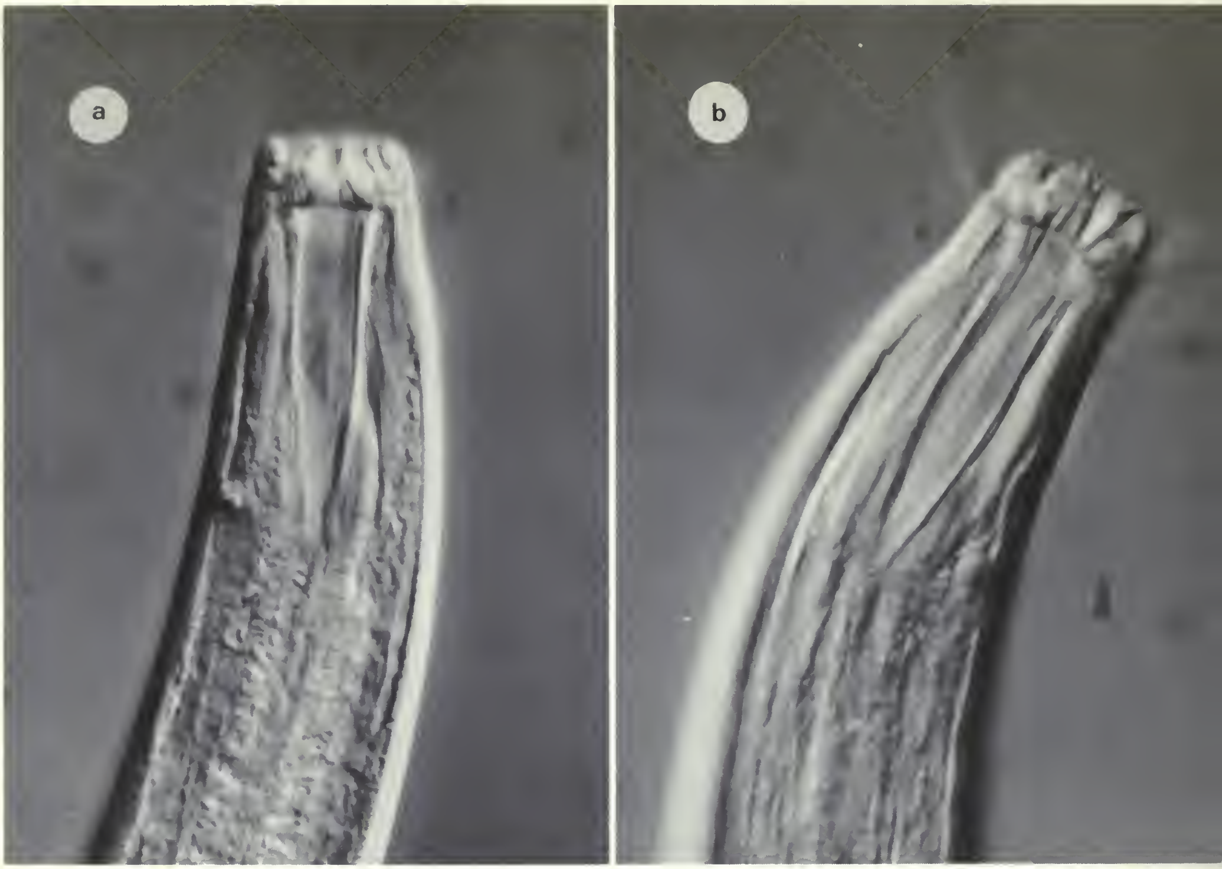

Fig. 4 (a) Left lateral view of female head showing subventral and subdorsal teeth, and subdorsal tooth like projection; (b) right lateral view of female head showing lateral tooth.

having 'six prominent bifid odontia'. As females of this genus appear indistinguishable it cannot safely be referred to either species and so to avoid zoogeographic problems it is here renamed *Odontophoroides hopperi* nom. nov. (type *Synodontium monhystera* sensu Hopper, 1968). It is characterized by the lack of lateral subcephalic setae at the base of the amphid and the absence of fine subcephalic setae associated with the subventral R_3 subcephalic setae. The discovery of further specimens, particularly males, should elucidate the relationship between *O. hopperi* and the European species but until such time the status of this species remains equivocal. As a consequence of this analysis the original generic diagnosis of *Odontophoroides* given by Boucher & Helléouët (1977) should be modified to include forms with or without lateral subcephalic setae.

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Notes on Atlantic Asteroidea. 2. Luidiidae

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Introduction

In reviewing the Atlantic species of Asteroidea, recent proposals for inclusion of the family Luidiidae in the order Paxillosida rather than the Platyasterida (as in the 'Treatise of Invertebrate Paleontology') need to be discussed. Also, several taxonomic complications to do with the large genus *Luidia* have become apparent, particularly in reassessing the ranks of similar taxa from the continental shelves on the two sides of the ocean. These are better disposed of in a preliminary paper.

The large collections of the *Pillsbury* and *Gerda* of the University of Miami from both sides of the tropical Atlantic have supplemented the material already in the British Museum (Natural History). Only *L. patriae* Bernasconi from Argentina is not available, so comments on its affinity with *L. scotti* Bell are based on the published description. The number of nominal species occurring in the Atlantic is reduced by synonymy or lowering to infraspecific rank from 17 to 11. Coverage of *L. atlantidea* Madsen, *L. barbadensis* Perrier, *L. ciliaris* (Philippi) and *L. senegalensis* (Lamarck), all of which are limited to either east or west, is restricted to inclusion in a tabular key of principal characters and an outline of the distribution. Also *L. clathrata* (Say) raises only a nomenclatural problem, being another species of limited range. A neotype for *L. alternata alternata* (Say) and a lectotype for *L. sarsi sarsi* (Düben & Koren) are designated and discussed.

The good size range of specimens from the Miami collections has allowed for some comments on post-metamorphosal growth changes.

Systematic account

LUIDIIDAE Sladen, 1889

Astropectinidae: Luidiinae Sladen, 1889 : 244.

Luidiidae: Verrill, 1899 : 201; Fisher, 1911 : 105; Bernasconi, 1943 : 2–3; Fell, 1963 : 433; Spencer & Wright, 1966 : U42; Downey, 1973 : 21; Blake, 1973 : 22–24 (pt); A. M. Clark & Courtman-Stock, 1976 : 43; McKnight, 1977 : 116; Blake, 1982 : 186.

AUTHORITY. Under Article 36 of the International Code of Nomenclature (coordinate categories), the authority and date of a name in the family group can originate from its use as a subfamily name, so the citation of Verrill, 1899 as author and date for Luidiidae (e.g. by Spencer & Wright in the 'Treatise on Invertebrate Paleontology', 1966) is incorrect.

ORDINAL POSITION. In 1963 Fell, followed by Spencer & Wright (1966) split off the Luidiidae to the order Platyasterida (otherwise including only the lower Palaeozoic family Palasteriscidae) from its longstanding position close to the Astropectinidae because of its transversely matching longitudinal series of adambulacral, actinal and inferomarginal plates. This has never seemed to me satisfactory in view of the close resemblance of *Luidia* and *Astropecten*, especially in transverse section of the arms, and I fully agree with Jangoux (1975) and McKnight (1977), who dismissed Fell's disposition because of close anatomical resemblances between *Luidia* and certain astropectinids, and the different alignment of the ambulacral and adambulacral plates (the Platasteriscidae having only a very shallow

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ambulacral groove, unlike any recent asteroids). The Luidiidae should therefore be included in the order Paxillosida Perrier, 1884, formerly lumped with Perrier's Valvatida in Sladen's larger order Phanerozonia (1889). Blake (1982) has independently reached the same conclusion on the basis of his more detailed morphological studies of the various series of ossicles, coupled with the absence of any fossil luidiids in pre-Miocene strata. The Luidiidae shares with the Astropectinidae not only the paxilliform abactinal plates but also the presence of superambulacral plates, the knobbed tube feet with double ampullae and the horizontal framework to the body of enlarged marginal plates (though this is not exclusive to the Paxillosida). The main differences are the lack of transverse matching of the actinal series with the adambulacrals and inferomarginals in astropectinids—a character probably not of more than familial weight—and the reduction and paxilliform nature in luidiids of the superomarginals, so that only their position matching the inferomarginals indicates their true identity. (In the Clathrata and Alternata groups of species of *Luidia*, the two lateralmost series of abactinal paxillae each side also match the marginals in length and are indistinguishable from the superomarginal paxillae unless the latter are broadened—which reaches an extreme development in *Luidia (Platasterias) latiradiata* (Gray), referred to the Clathrata group by Blake (1973); other groups of *Luidia* species have smaller lateral abactinal paxillae.)

DIAGNOSIS. A family of Paxillosida with 5–11 fairly long, gently tapering arms (usually described as 'strap-shaped'), not broadening basally into the disc; lower surface almost flat (and in preserved specimens often also the upper, owing to collapse of the fine paxillar reticulum); median paxillae irregular and smaller than the lateral ones, of which at least the two outermost series are arranged in longitudinal series and matched transversely; papulae distributed all over the upper side between the abactinal plates, compound at their outer ends; superomarginal plates paxilliform, similar in structure to the adjacent abactinal plates, though up to twice as long in species where the abactinal paxillae are particularly small (only in the subgenus *Platasterias* of *Luidia* are the superomarginals considerably broader than the lateral paxillae, though still essentially paxilliform); inferomarginal plates massive, lateral or lateroventral in position but never conspicuous in dorsal view, each raised into a flat-topped keel bearing some large spines, especially near the upper end (the ambitus or broadest part of the arm), interspersed with spinelets of varying size, the sides of the keel armed with many fine geometrically-arranged fasciolar spinules; a small actinal plate (rarely two proximally) intercalated between each inferomarginal and the matching adambulacral plate, often acting as the base for a spiniform pedicellaria (in a few species of the Alternata group of *Luidia* there are supernumerary reduced, pedicellaria-bearing actinal plates superimposed on the abradial ends of the adambulacral plates); interradial areas compact, rarely with more than a few series of actinal plates; adambulacral plates broad and raised into a shallow keel, bearing 2–4 large spines along the crest (the fourth, if present, proximal to the third), the innermost (furrow spine) compressed, curved and sabrelike; pedicellariae well developed, sessile, with 2-, 3- or even 4-valves, absent in a few species or individuals, those of the upper side usually nutcracker-like with broad blunt jaws, the marginal and ventral ones more elongated and spiniform; internally, superambulacral plates linking the ambulacrals and inferomarginals; tube feet pointed or ending in knobs, their internal ampullae double.

REMARKS. Döderlein (1920) monographed *Luidia* Forbes, 1839, distinguishing the following groups and subgenera:
Clathrata group: subgenera *Senegaster* and *Petalaster* Gray, 1840;
Alternata group: subgenera *Maculaster, Alternaster* and *Armaster*;
Quinaria group: subgenera *Integraster, Denudaster, Penangaster* and *Quinaster*;
Ciliaris group: subgenus *Hemicnemis* Müller & Troschel, 1840 (other names being Döderlein's).
Fell (1963) pointed out that the type species of both *Luidia* and *Hemicnemis* is *L. ciliaris* (Philippi) so that *Hemicnemis* is a synonym. Except for *Armaster*, which he lumped with

Alternaster, he perfunctorily raised all the others to generic rank, a move which has failed to gain acceptance, notably from Blake (1973) in an exhaustive study of the ossicles of luidiids and related asteroids. At the same time, Blake reduced *Platasterias* Gray, 1871 to the rank of a subgenus of *Luidia* (whereas Fell had included it in the subclass Somasteroidea), since *P. latiradiata* is undeniably more closely related to *Luidia clathrata* (Say) than *clathrata* is to *L. ciliaris*. The family is accordingly considered to be monogeneric.

Where Atlantic taxa of *Luidia* are concerned, the limits between Döderlein's main groups are particularly blurred. For instance, *L. scotti* Bell, 1917 (omitted by Döderlein), now treated as a subspecies of *L. ludwigi* Fisher which Döderlein put under the Alternata group, loses its bold colour pattern characteristic of that group soon after preservation and must have a different pigment to *L. alternata*. Since *L. ludwigi scotti*, together with *L. armata*, also lacks the enlarged abactinal spines found in the majority of species of the Alternata group, it bridges the gap to the similarly smooth species of the Clathrata group, both groups having the two outermost series of abactinal plates matching up with the marginal plates. *L. barbadensis* Perrier has the lateral paxillae only slightly outnumbering the marginals by *c.* 12/10, which serves to differentiate it from the two above groups as defined by Döderlein, who listed it as 'incertae sedis' under the Alternata group. Its coarse and squarish lateral paxillae certainly link it more closely with the Alternata group than with the Quinaria and Ciliaris groups with their finer and more numerous paxillae.

One of the main characters by which at least the Atlantic species of *Luidia* can be split up is the alignment of the inferomarginal plates, whether or not they extend above the ambitus. In the Clathrata and Alternata groups they are ventro-lateral (see Fig. 1a, b) but in the Quinaria and Ciliaris groups they extend higher. The difference in alignment is accompanied by some difference in armament. With more ventrally-aligned inferomarginals, the largest spines are at the ambitus and project horizontally, or nearly so (though if there is more than one ambital spine then the uppermost is more or less reduced); the spines below the ambitus are appreciably smaller also and are somewhat appressed. When the inferomarginals extend on to the upper surface all their spines are erect, the uppermost one (or two) being largest, the top one projecting almost vertically upwards in its natural position, at least on those (often alternate) plates where it arises from its highest locus.

Secondly, the number of lateral paxillae corresponding to the superomarginal ones—whether matching exactly or in excess—is another easily determined character, again dividing the Clathrata and Alternata groups from the Quinaria and Ciliaris ones, though *L. barbadensis* is an exceptional intermediate, as already mentioned.

These two characters are therefore the most important in the tabular key (table 1) to the Atlantic species, besides the obvious difference in arm number for some species. The occurrence of pedicellariae is variable and not reliable for more than local differences at the infraspecific level, though their location and the number of valves may be useful.

ONTOGENY. The reproduction and larval stages of *Luidia sarsi* were studied by Tattersall & Shepherd (1934). An early post-metamorphosal stage of this species is exemplified by the diminutive holotype, R 8 mm, of *Astrella simplex* Perrier, 1882, synonymized with *L. sarsi* by Ludwig (1897).

Fully metamorphosed specimens of other species taken by the *Pillsbury* in the tropical Atlantic show that all the primary plates, even the small actinal ones, occur from an early stage, though the actinals at first lack any armament.

At R *c.* 6 mm, the upperside paxillae of each arm consist of a band of somewhat irregular median paxillae flanked on either side by two complete regular longitudinal series, the outer of which is the superomarginal series and the other the primary lateral series. Almost immediately a secondary lateral series begins to develop proximally between the two but probably does not become fully developed to the arm tip until R is *c.* 25 mm, at least in *L. alternata numidica* Koehler. In *L. heterozona* Fisher, where the lateral paxillae are relatively smaller, the secondary lateral series is not initiated until R *c.* 25 mm and is still not quite complete at R 50 mm. At least in species with fairly coarse paxillae, the primary lateral

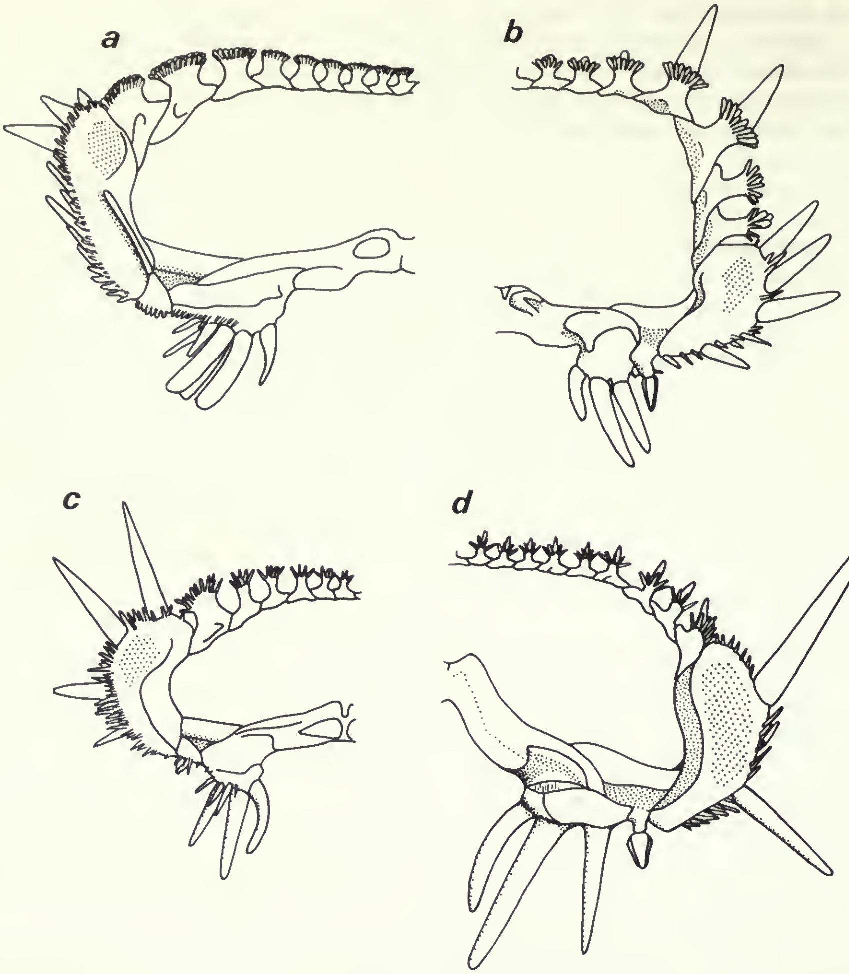

Fig. 1 Half arm sections, viewed from the proximal side, of: (a) *Luidia clathrata, Pillsbury* st. 652, R *c.* 120 mm; (b) *L. alternata alternata, Pillsbury* st. 767, R *c.* 90 mm; (c) *L. sarsi elegans. Albatross* st. 2177, R *c.* 115 mm; (d) *L. sagamina aciculata, Atlantide* st. 61, R *c.* 90 mm.

series can usually be recognised by the fact that both its abradial and adradial basal lobes are overlain by the opposing lobes of the secondary lateral and outermost median series of paxillae respectively (see Fig. 1a, b, d) but this does not always hold good when the skeleton is more delicate. The median paxillae also increase in number to some extent, less so in species where they are stouter, as in *L. alternata* (Say) where the total number of paxillae across the arm proximally between the two opposite superomarginal series increases from 9 or 10 at R 6 mm to only *c.* 12 or 13 at R 50 mm. There are still only *c.* 12 in the largest specimen of *L. alternata alternata* studied, R 175 mm, so the tabula of the larger paxillae in such species may be markedly broadened.

With regard to the armament, as usual in newly metamorphosed asteroids, the spinelets and future spines are all attenuated, often trifid, with the terminal point prolonged. This is still true up to R *c.* 9 mm, except for the furrow and second adambulacral spines, which are simple and unbranched, though still uniform in length with the other spinelets. At R *c.* 10 mm, an ambital inferomarginal spine begins to enlarge in *L. alternata* and the second adambulacral spine also increases disproportionately in size, while a few of the more lateral paxillae begin to develop a single large central spine. In species with a third adambulacral

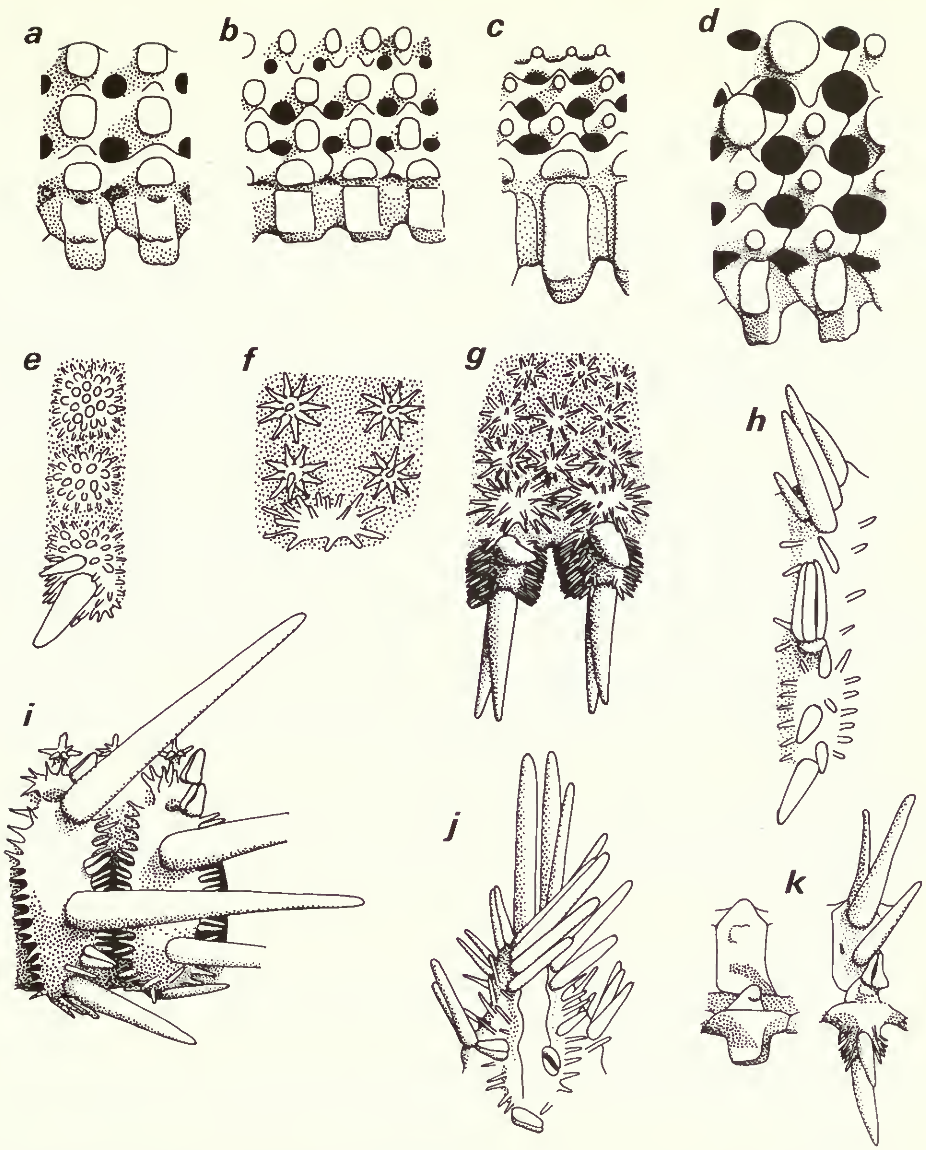

Fig. 2 (a to d) Dorsal views of a proximal part of an arm, showing the upper ends of several inferomarginals, the adjacent superomarginals and some abactinal plates, denuded: (a) *Luidia ludwigi scotti*, paratype, *Terra Nova* st. 42, R 62 mm; (b) *L. barbadensis, Gerda* st. 239, R *c.* 130 mm; (c) *L. sarsi elegans* (as in Fig. 1c); (d) *L. alternata alternata, Pillsbury* st. 767, R *c.* 75 mm; (e to g) the same views with armament entire (inferomarginal omitted in (f)) of: (e) *L. ludwigi scotti* (as in Fig. 2a); (f) *L. heterozona barimae, Pillsbury* st. 652, R 200+ mm; (g) *L. sarsi africana,* Namibia, R *c.* 100 mm; (h) one adambulacral, actinal and inferomarginal, in ventral view of *L. alternata alternata* (as in Fig. 1b); (i) *L. heterozona heterozona, Pillsbury* st. 24, R 100+ mm, lateral view of two successive inferomarginals and superomarginals with a few lateral paxillae; (j) apex of jaw of *L. heterozona barimae* (as in Fig. 2f); (k) *L. sagamina aciculata*, (as in Fig. 1d), two lines of adambulacral, actinal and inferomarginal plates, the one on the left denuded. The proximal side is to the right in (a–g), to the left in (h, i & k).

Table 1 Tabular key to the Atlantic species of *Luidia*. Entries in brackets signify occasional occurrence.

	1	2	3	4	5	6	7	8	9	10	11
senegalensis	9(8)	–	10	c	–	vl	–	2	4	–	–
clathrata	5	–	10	c	–	vl	–	2(3)	4	–	–
ludwigi scotti	5	+	10	c(s)	–	vl	–	2(1)	4	3	–
patriae	5	–?	10	u	–	vl	–	2	4	–	–
alternata (2 subspp.)	5	+	10	S	–	vl	–	2,3	3(½)	3	–
barbadensis	6	–	12–13	c	–	vl	–	3(2)	4	3	–
sagamina aciculata	5	–	16–19	s	+	l	+	2/3	2(3)	3	+
heterozona (2 subspp.)	10	–	15–18	u	+	l	+	3/2,4/3	(4)3	2	+
sarsi (3 subspp.)	5	–	17–20	u	+	l	+/–	4/3,3/2	3(½)	2	+(–)
atlantidea	5	–	15–19	c	–	l	+/–	3/2(4)	3(½)	2	+(–)
ciliaris	7(8)	–	15–18	c	(+)	l	+	3–5	2	–/3	–

1. Arm number.
2. Colour pattern of upper side:
   + — patchy (may fade in long-preserved *L. ludwigi scotti*).
   – — uniform or darker along midradial area or lighter along midradial area or lighter along superomarginal or adjoining lateral paxillae.
3. Number of consecutive lateral paxillae corresponding to 10 superomarginal ones.
4. Paxillar armament:
   c — central spinelets distinctly coarser than peripheral ones.
   u — central and peripheral spinelets uniform.
   s — one central spinelet both longer and stouter on most paxillae.
   S — one central spine (1–5 mm long) abruptly enlarged on some scattered (mostly lateral) paxillae.
5. Shape of superomarginal paxillae:
   + — elongate.
   – — rounded or squarish.
6. Alignment of inferomarginal plates:
   l — lateral.
   vl — ventro-lateral.
7. Inferomarginal spines:
   + — alternating on consecutive plates.
   – — all on the same levels.
8. Number of large erect inferomarginal spines.
9. Number of adambulacral spines.
10. Number of valves on actinal pedicellariae (when present, – = absent).
11. Oral furrow pedicellariae:
    + — present.
    – — absent.

spine in the adult, this is probably evident proximally by R 12–15 mm and the other spines and spinelets grow and coarsen into their adult proportions at this size or soon after. *Luidia sagamina aciculata* Mortensen is exceptional in the development of the third adambulacral spine, which may be lacking altogether, especially in american specimens, judging from the few so far studied. Increase in numbers of spines also shows a growth gradient along the arm. In *L. heterozona* Fisher, for instance, only about four proximal adambulacral plates have the third spine enlarged at R 20 mm but there is even a fourth spine on the first 10–15 plates, and almost equal to the fully developed third one, by R *c.* 80 mm.

Actinal and abactinal pedicellariae, when developed, probably first appear between R 15 and 20 mm but oral furrow pedicellariae, for example in *L. heterozona*, are not fully modified from pairs of spines until R exceeds *c.* 50 mm.

PREVIOUS WORKS. Useful relevant publications on the Luidiidae include the general monograph of Döderlein (1920), Nataf & Cherbonnier (1973) on the tropical West African area and Downey (1973) and Walenkamp (1976 and 1979) on the West Indian area.

DISTRIBUTION. The species of *Luidia* are mostly restricted to the shelf, though several Atlantic taxa extend to the upper bathyal, including *L. barbadensis* to 430 metres, *L. ciliaris* to 400 metres, *L. heterozona* and *L. sagamina aciculata* to 975 metres and *L. sarsi* exceptionally to 1300 metres. (The maximum depth for both *L. heterozona* and *L. sagamina aciculata* derives from *Jean Charcot* (Walda cruise) st. 40, *c.* 04° 07′ N, 01° 35′ W, off Ghana, 975 metres, and is surprising since previous maxima for the two respectively were only 400 and 150 metres, cited by Nataf & Cherbonnier (1973), the vast majority of records for both species being from 50–100 metres.)

Geographically, five Atlantic taxa appear to be restricted to the american side of the ocean, namely *L. barbadensis, L. clathrata, L. ludwigi scotti, L. patriae* and *L. senegalensis* (the last despite its name), while *L. atlantidea* and *L. ciliaris* are entirely eastern (american records for *L. atlantidea* proving incorrect, see p. 168. The remainder are distributed as follows:

WEST ATLANTIC	EAST ATLANTIC
alternata—N Carolina to N Argentina	*numidica*—Senegal to Zaire (Congo)
barimae—Venezuela to French Guiana	*heterozona*—Mauritania to Angola
sagamina aciculata(?)—N Carolina to Florida Strait	*sagamina aciculata*—Mauritania to Zaire & St Helena
elegans—E U.S.A. & Gulf of Mexico	*sarsi*—Norway to Mauritania & Azores
elegans(?)—S Brazil	*africana*—SW & S of southern Africa

The relationships of these are discussed below to assess their respective ranks.

LUIDIA Forbes

Luidia Forbes, 1839 : 123; Sladen, 1889 : 244–248; Fisher, 1911 : 105; Süssbach & Breckner, 1911 : 198; Döderlein, 1920 : 193–246; Bernasconi, 1943 : 3–5; A. M. Clark, 1953 : 379–380; Fell, 1963 : 433; Downey, 1973 : 21–22; Tommasi, 1974 : 7; A. M. Clark & Courtman-Stock, 1976 : 43. Type species: *Luidia fragilissima* Forbes, 1839 (a synonym of *Asterias ciliaris* Philippi, 1837), by monotypy.

Hemicnemis Müller & Troschel, 1840 : 105; Döderlein, 1920 : 217 (as subgenus). Type species: *Asterias ciliaris* Philippi, 1837.

Petalaster Gray, 1840 : 183: Döderlein, 1920 : 215 (as subgenus). Type species: *P. hardwicki* Gray, 1840, cited by Fisher, 1911 (though with *Petalaster* in synonymy), non *P. columbia* Gray, designated by Fell, 1963.

Luydia (lapsus) Düben & Koren, 1846 : 254.

Astrella Perrier *in* Milne-Edwards, 1882 : 21. Type species: *A. simplex* Perrier, 1882 (a synonym of *Luidia sarsi* Düben & Koren, 1845), by monotypy.

Senegaster, Maculaster, Alternaster, Armaster, Integraster, Denudaster, Penangaster & Quinaster (subgenera) Döderlein, 1920 : 215–217, raised to generic rank by Fell, 433–434 (except for *Armaster*).

Luidia alternata (Say)

Figs 1b, 2d, h, 3a–i, 4, 5

Asterias alternata Say, 1825 : 144–145.

Luidia alternata: Lütken, 1859 : 42–43; Perrier, 1875 : 334–336 [1876 : 254–256]; Sladen, 1889 : 250–251, 740; Verrill, 1915 : 201–203 [non *L. alternata bicolor*]; Döderlein, 1920 : 241, 267–268, figs 7, 11; H. L. Clark, 1933 : 20, pl. 1; Bernasconi, 1943 : 14–15, pl. 3, figs 1, 6, pl. 4, fig. 1; Engel & Schroevers, 1960 : 6; Ummels, 1963 : 97–98, pls 8, 10; Gray, Downey & Cerame-Vivas, 1968 : 138, fig. 6; Tommasi, 1970 : 8, pl. 8, fig. 24; Downey, 1973 : 23–24, pl. 2, figs A, B; Blake, 1973 : 33–34, pl. 6, figs 25–42; Walenkamp, 1976 : 29–32, figs 6, 7, pl. 3, fig. 3, pl. 4, fig. 4.

Luidia granulosa Perrier, 1869 : 109–110, pl. 2, fig. 18.

Luidia variegata Perrier, 1875 : 337 [1876 : 257].

Luidia numidica Koehler, 1911 : 3, pl. 1, figs 8–11; 1914 : 167, pl. 4, fig. 7; Döderlein, 1920 : 235, 242; Nataf & Cherbonnier, 1973 : 71–74, pl. 1, figs A, C, pl. 5, figs 1, 2, pl. 7, fig. 6, pl. 9, figs A–D.

Luidia quequenensis Bernasconi, 1942 : 253; 1943 : 15–18, pl. 2, fig. 4, pl. 3, figs 2, 3, 7, pl. 5, figs 1, 2; 1960 : 21–22, pl. 3, fig. 1; Carrera-Rodriguez & Tommasi, 1977 : 65.

Luidia bernasconiae A. H. Clark, 1945 : 19–21; Gray, Downey & Cerame-Vivas, 1968 [?pt] : 138, fig. 7; Downey, 1973 : 25.

Luidia alternata var. *numidica*: Madsen, 1950 : 206–209, fig. 9.

Luidia alternata numidica: A. M. Clark, 1953 : 388–389, pl. 41, fig. 1; 1955 : 22; Engel & Croes, 1960 : 11–12, pl. 6, figs. 1, 2.

R up to 175 mm. R/r ranging from *c.* 5–6/1 at R 30–40 mm to 7–9/1 at R > 70 mm.

A species of *Luidia* with normally 5 arms; abactinal paxillae with about 4 longitudinal series each side also forming transverse rows with the matching but distinctly smaller superomarginal paxillae, though irregularities may occur where the paxillae of the second and third (sometimes other series) are markedly enlarged and bear a single stout central spine fringed by usually several rings of spinelets, the large spines similar in magnitude to the ambital inferomarginal spines, rarely some of the lateralmost series and many of the median paxillae may have a smaller central spine developed; inferomarginal plates primarily ventral in position, only narrowly visible dorsally, armed at the ambitus with 2 or 3 large spines, usually projecting approximately horizontally, and on the ventral side with 2–4 smaller and somewhat flattened spines among the spinelets: adambulacral plates with 3 large spines in a row at right angles to the furrow, sometimes a more or less enlarged spine proximal to the lateralmost one; elongate, 3- or 4-valved pedicellariae, present on some proximal actinal plates (rarely also on the outer ends of the first few adambulacral plates) the slender valves usually only meeting at the tips; shorter, more often bivalved pedicellariae sometimes present (especially in west african specimens) on some abactinal and/or superomarginal paxillae, no pedicellariae on the furrow face of the oral plates. Colour boldly patterned on the upper side with a dark pentagon on the disc and three to five transverse dark bands, brown, black, greenish or purple, on each arm, the remainder being yellow, cream or white.

STATUS OF *L. numidica.* Madsen (1950) treated *Luidia numidica* Koehler as a west african variety of *L. alternata* and noted that the only difference appeared to be the smaller number of spine-bearing paxillae in *numidica*. A. M. Clark (1953) used subspecific rank for *numidica* but noted that a specimen from the Cape Verde Islands with relatively numerous spino-paxillae is very similar to some west Atlantic specimens of *L. alternata*. In 1973, Nataf & Cherbonnier treated *numidica* as a full species but without comparisons or any comment on its status.

Koehler (1911) had only two specimens from West Africa, a poor dry one with R 52 mm and the broken holotype, r 13 mm so R probably 80–100 mm. He remarked on the closeness to *L. alternata* but distinguished that species by the more numerous inferomarginal and paxillar spines, the more attenuated pedicellariae and the 'quite different' paxillae with the peripheral spinelets thin and elongated, not short, thick and granuliform. Study of *c.* 30 and 15 specimens from west and east Atlantic respectively, mostly from the *Gerda* and *Pillsbury* collections, now indicates that, although the armament of the paxillae is somewhat variable in both east and west Atlantic specimens and is also subject to some extent to growth changes, there is a consistent difference in the armament of the smaller paxillae if total size is taken into account and also a significant difference in the number (often also the shape) of the large paxillar spines. Already in west african specimens at R 20–25 mm, over half the median paxillae have more than one (usually 2–4) short coarse similar central spinelets; at R 40–50 mm these number 3–6 and at R *c.* 60 mm usually 4–8 (see Fig. 3h, i). In *L. alternata* from the western Atlantic, even at R 100 mm or more, many central paxillae still only have a single more or less coarser central spinelet, the maximum number being about 4. However, these large specimens may have some median paxillae with the peripheral spinelets arranged in two concentric rings of 6–10 each, the outer ones being more slender and cylindrical than the inner ring, the spinelets of which are transitional in shape to the central spinelet (or spine). In general, the shape of the peripheral spinelets can usually be called subclavate but

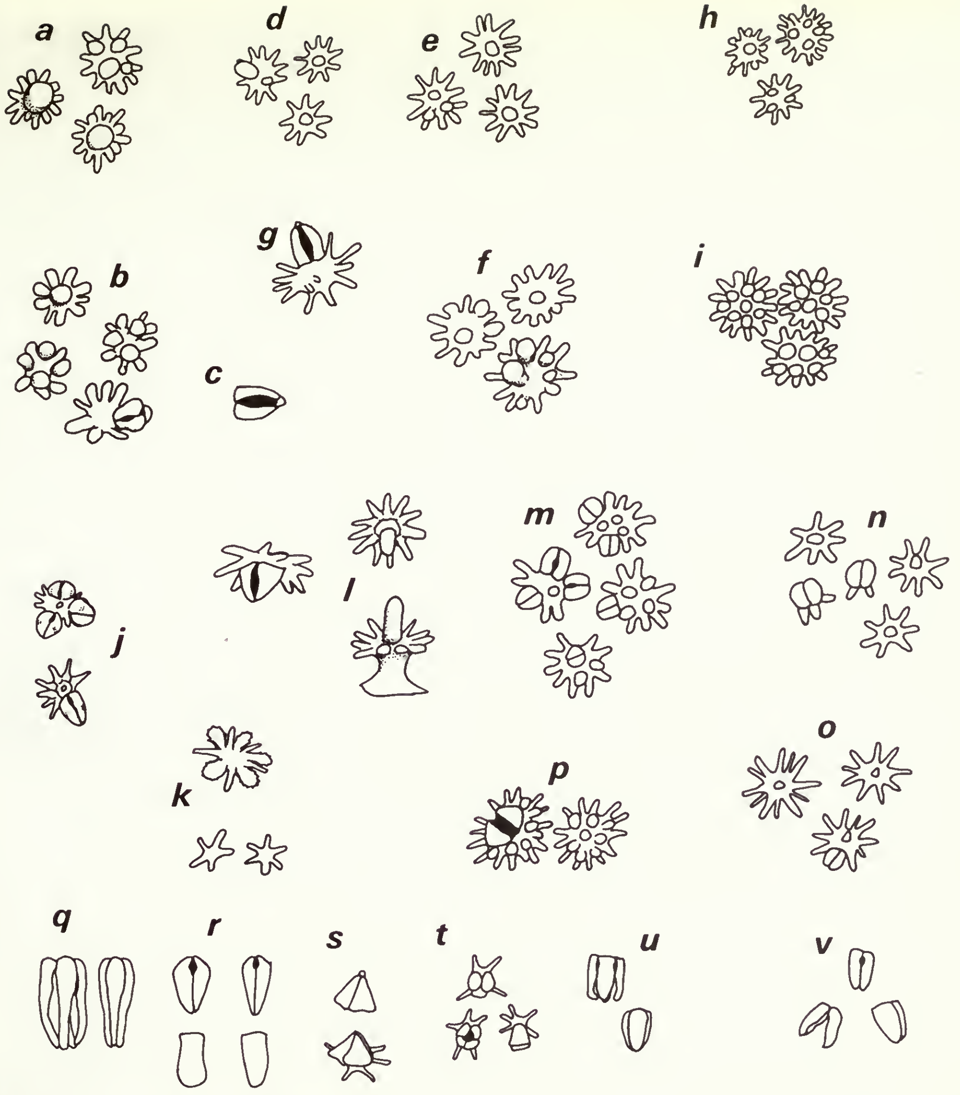

Fig. 3 (a, b, d–p) Abactinal paxillae, (c, q–v) pedicellariae. (a–g) *Luidia alternata alternata*, (a) type material of *L. quequenensis*, Quequen, N Argentina, R 72 mm, median paxillae; (b) holotype of *L. bernasconiae*, R 100 mm; (c) the same, superomarginal pedicellaria; (d) *Gerda* st. 1038, R 40 mm, median paxillae; (e) *Oregon* st. 4215, R *c.* 60 mm, median paxillae; (f) *Pillsbury* st. 654, R 100+ mm; (g) *Pillsbury* st. 767, R *c.* 90 mm, superomarginal paxilla; (h, i) *L. alternata numidica*: (h) *Pillsbury* st. 248, R only *c.* 22 mm; (i) Cape Verde Is, R 55–60 mm; (j) *L. heterozona heterozona, Pillsbury* st. 68, R *c.* 100 mm, disc paxillae; (k) *L. ciliaris*, Naples, R 140 mm, inner lateral paxilla (above) and two median paxillae; (l) *L. sagamina aciculata, Atlantide* st. 61, R *c.* 90 mm, superomarginal paxilla (left) and lateral paxillae from above and the side (below); (m) *L. sarsi sarsi*, W. of Scotland, R *c.* 100 mm, median paxillae; (n) *L. sarsi sarsi*, paratype of *L. africana, Porcupine* st. 36, R *c.* 85 mm, disc paxillae; (o) *L. sarsi elegans, Gerda* st 456, R *c.* 60 mm, median paxillae; (p) *L. atlantidea, Pillsbury* st. 26, R *c.* 100 mm, lateral paxillae; (q) *L. alternata alternata, Oregon* st. 4190, actinal pedicellariae; (r) *L. heterozona heterozona, Pillsbury* st. 259 (left) and 49 (right), actinal pedicellariae in two views; (s) *L. sagamina aciculata, Atlantide* st. 61, two actinal plates, one armed only by the pedicellaria, pedicellariae slightly foreshortened; (t) *L. ludwigi scotti*, paratype, actinal paxillae with 2-, 3- and 4-valved pedicellariae, foreshortened; (u) *L. ludwigi scotti, Pillsbury* sts 1384 & 842, lateral views of 4- and 3-valved actinal pedicellariae; (v) *L. sarsi sarsi*, Shetland Is, lateral views of actinal pedicellariae.

alternate ones may be hardly at all expanded at the tips on the slightly larger paxillae. As for the large paxillar spines on the second and third lateral series of paxillae particularly, even in the Cape Verde Islands specimen mentioned in 1953 only *c.* 35%, at most, of these lateral paxillae have the large spines. In other specimens from West Africa the percentage is usually *c.* 20. The shape of the spines is also relatively squat, their length most often 1–2 mm, the longest (in Koehler's large holotype) 3 mm, the length/basal breadth usually less than 3/1. In american specimens such squat spines may also occur but usually the length/breadth ratio is 4·0–4·5/1 and the length may exceed 3 mm even at R only 60 mm.

The conclusion reached from these observations is that the specimens from the two sides of the Atlantic are conspecific but the west african form can be recognized as a distinct subspecies *numidica* of *L. alternata*, distinguished by the more 'plushy' superficial appearance of the abactinal paxillae, interspersed with shorter and fewer large spines.

SYNONYMY. *Luidia granulosa* Perrier, 1869 was recognized as a synonym of *L. alternata* by Perrier himself in 1875 and *L. variegata* Perrier, 1875 by Verrill, 1915. In 1950, Madsen (cited by A. M. C., 1953 : 380) also referred *L. bernasconiae* A. H. Clark, 1945, to the synonymy but this was refuted by Downey in 1968 & 1973, who maintained that it has only two adambulacral spines, not three or four, and the non-spine-bearing paxillae have 5–10 clavate peripheral spinelets compared with 10–16 slender acute ones in *alternata*, though on p. 23 of the 1973 paper she describes the peripheral paxillar armament of *alternata* as subclavate. The dried holotype of *L. bernasconiae* certainly shows swollen-tipped peripheral paxillar spinelets more clavate than usual for *L. alternata* but it regularly has three large and a fourth smaller adambulacral spine, as described by A. H. Clark, the common number for *L. alternata*. In view of the variability in shape of the paxillar armament in *L. alternata* already mentioned, it is difficult to maintain *bernasconiae* as distinct. If there are specimens from North Carolina as described by Gray, Downey & Cerame-Vivas (1968) with sporadic large spines but only two adambulacral spines, then these may have to be nomenclatorially distinguished but not as *L. bernasconiae*. The superficial difference in proportions between *L. alternata* and *L. bernasconiae* suggested by the photographs in the 1968 paper is correlated with the much larger size (R *c.* 135 mm, judging from the scale) of the specimen named *alternata*, and exaggerated by the greater reduction so that both appear of similar size though R is only *c.* 77 mm in the specimen named *L. bernasconiae*.

With regard to *Luidia quequenensis* (and other species of *Luidia* described by her) Bernasconi, 1942 confusingly modified the terminology of the lateral abactinal paxillae used by Döderlein (1920, see pl. 18, caption) as follows: his 'Randpaxillen' (i.e. the superomarginal paxillae) become her 'paxilas marginales'; his 'untere Seitenpaxillen' (the two [primary and secondary] outermost series of lateral paxillae) become her 'paxilas inferomarginales'; his 'obere Seitenpaxillen' (the third and fourth series or two outer series of median paxillae) become her 'paxilas superomarginales'. This odd terminology has unfortunately been perpetuated by Carrera-Rodriguez & Tommasi (1977). Bernasconi distinguished *L. quequenensis* from *L. alternata* in 1943 (pp. 5, 17) by the large number and coarse shape of the spines of the 'paxilas superomarginales', which should be the third and fourth series of paxillae from the true superomarginal ones. However, a specimen from Quequen, kindly presented to the British Museum by Dr Bernasconi, shows numerous spinopaxillae but more of these are in the second from outermost lateral series (what I call the primary row), though the third series also has a considerable number. However, there are many inconspicuous spineless paxillae also in these series so that even the second only has *c.* 64% of spinopaxillae out of well over 100 paxillae counted on several arms. The largest number of consecutive spinopaxillae found was only 9. Similar frequencies of over 60% of spinopaxillae in the second or third lateral series may occur throughout the range of *L. alternata alternata*, for instance in some of the *Challenger* specimens from Bahia, NE Brazil, others from French Guiana (*Oregon* and *Pillsbury* collections) and from Georgia (the holotype of *L. bernasconiae*).

NEOTYPE. In the event of future disagreement with the synonymies now proposed and in the

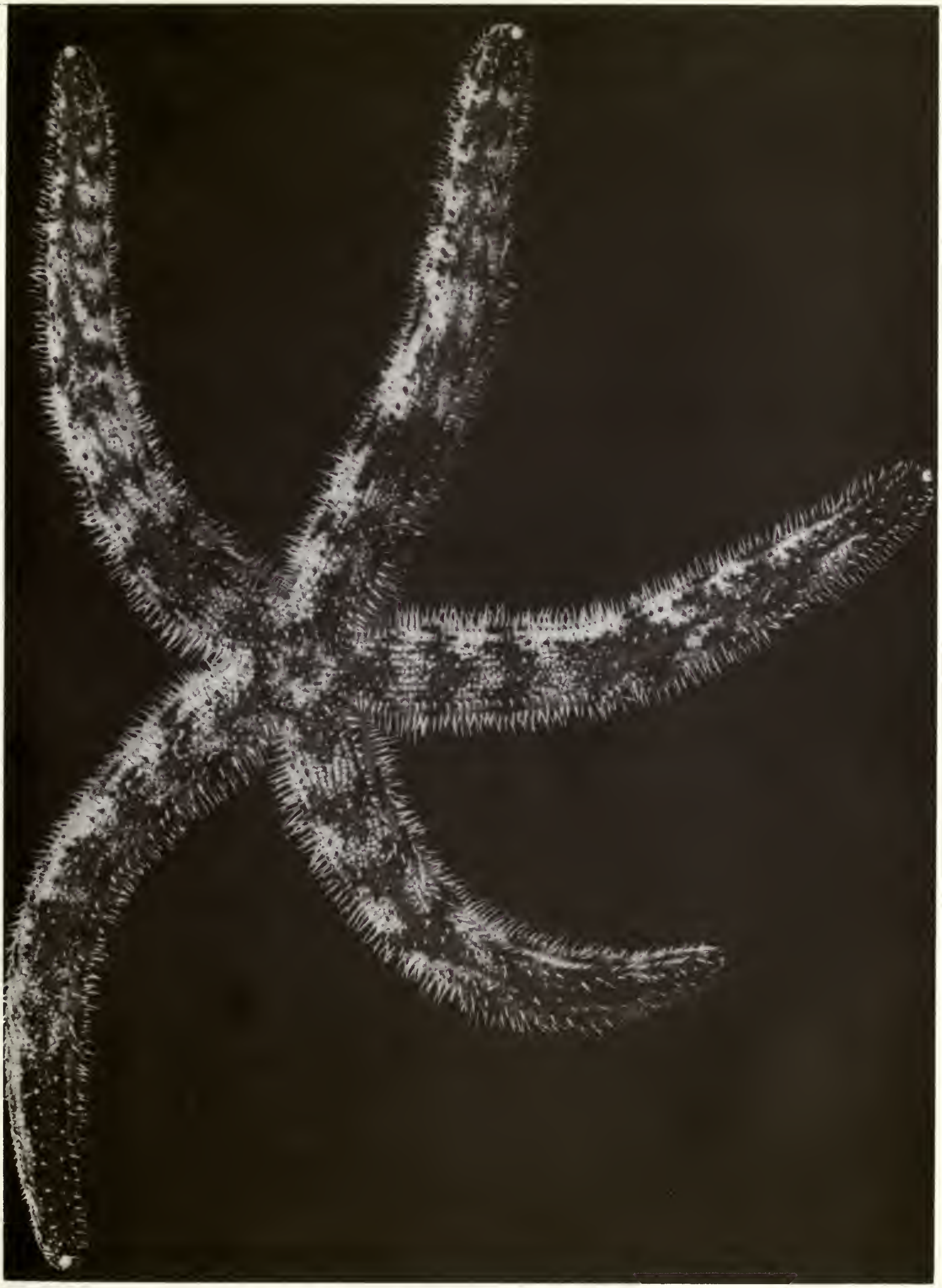

Fig. 4 *Luidia alternata alternata* (Say), neotype, BM(NH) reg. no. 1937.5.9.6, Dry Tortugas. Dorsal view, × 0·6.

absence of Say's type material (apparently long-lost), it is very desirable that a neotype from the vicinity of Florida, the type locality, should be nominated. Accordingly I propose a beautiful specimen from the Dry Tortugas now in the British Museum collections, registered number 1937.5.9.6, collected by Colman and Tandy, shown in Figs 4 and 5.

The arms vary in length so that R ranges from 150–175 mm; r is *c.* 19 mm and R/r = 7·9–9·2/1. Spinopaxillae are fairly numerous on the proximal primary (second) lateral series but become more sporadic distally (*c.* 55% of 100+ primary paxillae from proximal parts of several arms are spine-bearing). The longest spines measure 4·0 mm in length. Progressively fewer of the third, fourth and fifth series of paxillae are also enlarged with spines but none of the first series or the adjoining superomarginal paxillae and very few midradial paxillae. The median paxillae without enlarged spines have at least one central and about 9 peripheral spinelets, the latter almost cylindrical and blunt-tipped but the slightly larger paxillae have up to 4 central and *c.* 20 peripheral spinelets, the latter in a double ring of which the inner ones are subclavate and transitional in shape to the shorter, coarser central spinelets. The inferomarginal plates mostly bear two large ambital spines up to 7 mm long, slightly irregular in position on consecutive plates but not regularly alternating. There are 2–4, usually 3, more irregular smaller spines on the ventral side of each plate. Most of the primary actinal plates bear a long slender 3- or sometimes 4-valved pedicellaria and proximally also one or two additional pedicellariae based on supernumerary platelets superimposed on the lateral ends of the adambulacral plates. Most adambulacral plates have 3 large spines and a smaller fourth one proximal to the third (lateral-most). On the proximal plates this fourth spine may reach a similar length to the others.

DISTRIBUTION. *L. alternata alternata* from North Carolina to northern Argentina (*c.* 38° S); 0–160 metres.

L. alternata numidica from Senegal to Zaire (Congo), West Africa; 10–100 metres.

Luidia atlantidea Madsen

Fig. 3p

Luidia africana: Koehler, 1911 : 19; Döderlein, 1920 : 288–289; Mortensen, 1925 (pt) : 178. [Non *L. africana* Sladen, 1889.]
Luidia atlantidea Madsen, 1950 : 192–198, fig. 5, pl. 16, figs 1, 2; A. M. Clark, 1953 : 393, 394; 1955 : 22, 32; Nataf & Cherbonnier, 1973 : 76–80, pl. 1, fig. B, pl. 2, figs A, B, pl. 7, figs 1–5, pl. 9, figs E, F. [Non *L. atlantidea*: Downey, 1973 : 25 = *L. sagamina aciculata*.]
Luidia sarsi: Studer, 1884 : 43. [Non *L. sarsi* Düben & Koren, 1845.]

DISTRIBUTION. On re-examination, the specimen from North Carolina mentioned under the name of *L. atlantidea* by Downey (1973) proved to be *L. sagamina aciculata*. It has a white band along each side of the paxillar area on the arms but this is situated on the two regular rows of *lateral* paxillae, not on the superomarginal series as in *L. atlantidea*. It has not been possible to check the Halpern record cited by Downey but the likelihood is that this too would have been a similar misidentification.

The species is recorded from Atlantic Morocco to Zaire, including the Cape Verde Islands, 10–80 metres.

Luidia barbadensis Perrier

Fig. 2b

Luidia barbadensis Perrier, 1881 : 29; 1884 : 267 [non pl. 10, figs 7, 8, probabaly = *L. sarsi elegans*]; Verrill, 1915 : 205–207, pl. 24, fig. 1; Döderlein, 1920 : 216; H. L. Clark, 1941 : 25; John & A. M. Clark, 1954 : 145; Cherbonnier, 1959 : 170, fig. 3B, E, fig. 4; Downey, 1973 : 24–25; Carrera-Rodriguez & Tommasi, 1977 : 67–71, figs 5–9.
Luidia convexiuscula Perrier, 1881 : 30; 1884 : 268, pl. 10, fig. 6; Verrill, 1915 : 207.

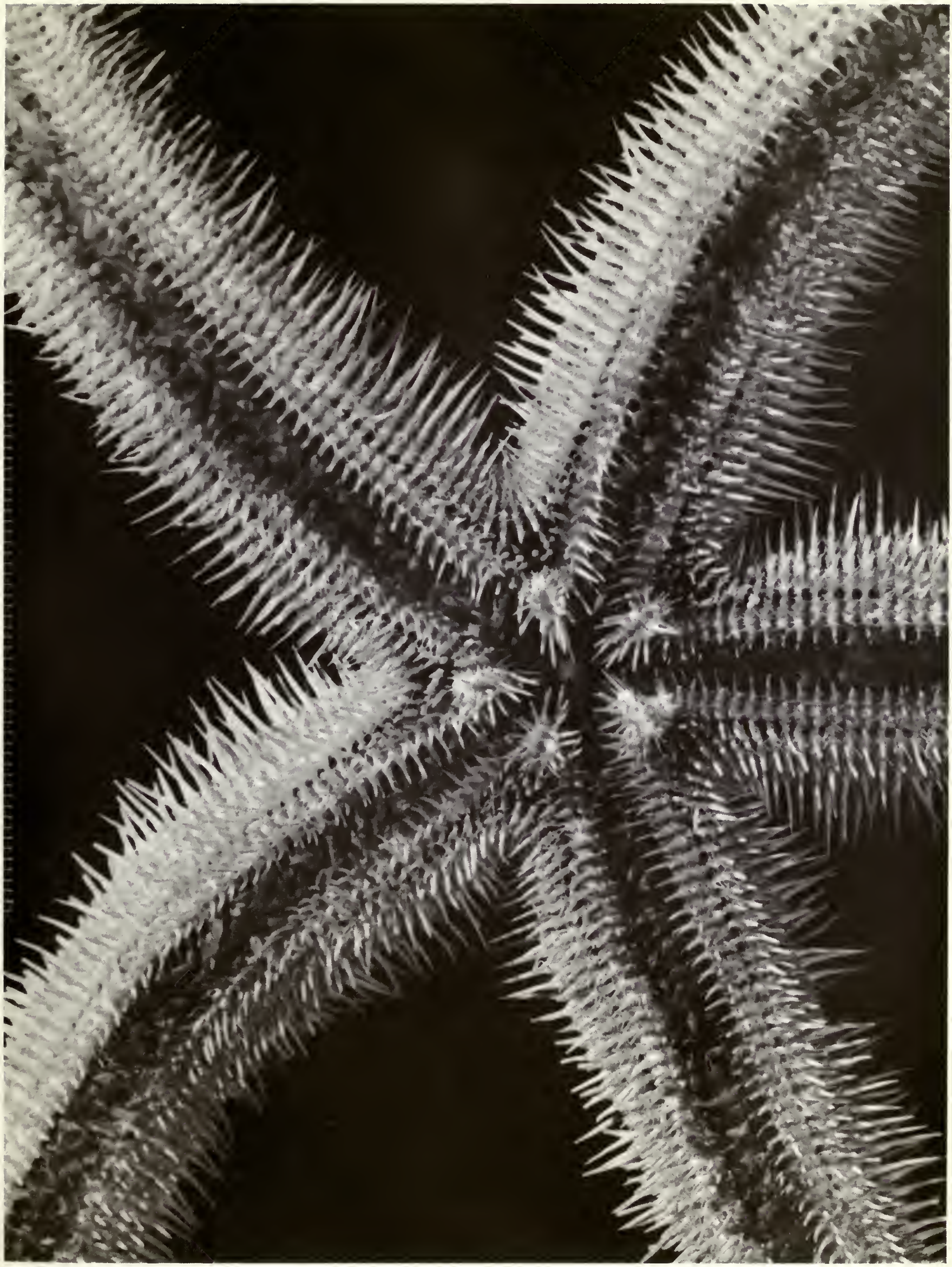

Fig. 5 *Luidia alternata alternata*, neotype. Ventral view of proximal part. × 1·7.

REMARKS. Records of five-armed specimens of *L. barbadensis* are probably based on specimens of *L. sarsi elegans*, which is partially sympatric with it. Certainly the five-armed specimen captioned as *L. barbadensis* by Perrier, 1884, pl. 10, figs 7, 8, appears to be *elegans*, which also differs in the much finer paxillae and the long marginal spines. All 36 *Gerda, Pillsbury* and *Oregon* specimens of *barbadensis* which I have seen have 6 arms.

DISTRIBUTION. Southern Florida and the immediately adjacent Gulf of Mexico, southern Bahamas, to SW Caribbean off Nicaragua and east and south to southern Brazil (*c.* 30° S), 73–430 metres.

Luidia ciliaris (Philippi)

Fig. 3k

Asterias ciliaris Philippi, 1837 : 144.
Luidia fragilissima Forbes, 1839 : 123; 1841 (pt) : 135–140, fig. on p. 135 [7-armed specimens].
Hemicnemis ciliaris: Müller & Troschel, 1840 : 104.
Luidia ciliaris: Perrier, 1875 : 342 [1876 : 262]; Sladen, 1889 : 254; Ludwig, 1897 : 61–85, pl. 4, figs 1, 2, pl. 6, figs 25–36; Süssbach & Breckner, 1911 : 209–210; Döderlein, 1920 : 287, figs 8, 17, 34; Koehler, 1921 : 55, fig. 41; Mortensen, 1927 : 90, fig. 89a; Madsen, 1950 : 205–206, fig. 8; Ursin, 1960 : 30–31; Tortonese, 1965 : 148–150, fig. 68; Blake, 1973 : 40, pl. 10, figs 1–26.

DISTRIBUTION. NE Atlantic, from southern Norway, the Skagerrak, Shetlands, Faeroe Channel, south to the Canary Islands and Azores (?Cape Verde Islands); 1–400 metres.

Luidia clathrata (Say)

Fig. 1a

Asterias clathrata Say, 1825 : 142. [Non *A. clathrata* Pennant, 1777.]
Luidia clathrata: Lütken, 1859 : 37–39; Perrier, 1875 : 332–333 [1876 : 252]; Sladen, 1889 : 253; Verrill, 1915 : 200–201, pl. 24, fig. 2; Döderlein, 1920 : 238, 239, 251–252, figs 1, 21; H. L. Clark, 1933 : 19–20; Bernasconi, 1943 : 6–7, pl. 2, fig. 1; A. H. Clark, 1954 : 375; Ummels, 1963 : 95–97, pls 10, 11; Gray, Downey & Cerame-Vivas, 1968 : 139, fig. 8; Downey, 1973 : 22–23, pl. 1, figs C, D; Blake, 1973 : 30–31, pl. 3, figs 1–28; Walenkamp, 1976 : 19–25, figs 2–4, 19a, pl. 3, fig. 2; 1979 : 11–12.

NOMENCLATURE. Although A. H. Clark (1954) pointed out that *Asterias clathrata* Say was preoccupied by Pennant's earlier senior homonym, he commented that 'nothing would be gained by displacing this well established name' and so continued to use it for this common West Indian species. Unfortunately, under the rules of nomenclature (Article 59(a)) such a junior primary homonym 'must be permanently rejected', that is unless the International Commission can be prevailed upon to use its plenary powers to suppress the earlier name (itself a synonym of *Asterias rubens* Linnaeus, 1758), which action is being requested in a separate proposal.

DISTRIBUTION. North Carolina (??New Jersey), Bermuda and the Gulf of Mexico to southern Brazil (*c.* 31° S); 0–175 metres but rarely below 70 metres.

Luidia heterozona Fisher

Figs 2f, i, j, 3j, r

Luidia heterozona Fisher, 1940 : 265–268, fig. M4, pl. 23; Madsen, 1950 : 203–205; John & A. M. Clark, 1954 : 148; A. M. Clark, 1955 : 33; Cherbonnier, 1963 : 182; Nataf & Cherbonnier, 1973 : 74–76, pl. 4, figs A, B, pl. 5, figs 3–6, pl. 9, figs I, J; Sibuet, 1975 : 284, 288.
Luidia mortenseni Cadenat, 1941 : 53–67, figs 1–3; Cherbonnier, 1963 : 182.
Luidia barimae John & A. M. Clark, 1954 : 145–148, figs 3, 4, pl. 6, fig. 2; Downey, 1973 : 25; Walenkamp, 1976 : 18–19, pl. 1, figs 1–3.

R up to 255 mm; R/r 7–11/1. Of over 150 specimens from both sides of the Atlantic taken by the *Gerda, Pillsbury* and *Oregon*, three have 9 arms, all the rest 10, though Madsen (1950) found 2 of the 37 *Atlantide* specimens to have 9 arms and another only 8.

A species of *Luidia* with usually 10 arms, relatively slender and attenuated; abactinal paxillae all relatively small and rounded but rather variable in size medially, some slightly larger ones intermingled; laterally two matching longitudinal series each side, outnumbering the adjacent more elongate superomarginal paxillae by 15–18/10; inferomarginal plates mainly lateral in alignment, bearing up to four spines in *L. heterozona barimae* but rarely more than three in *L. heterozona heterozona*, the spines erect, long and acute, the uppermost (at least on alternate plates) projecting vertically upwards and the uppermost or the second the longest, the spines alternating fairly regularly in level on successive plates and often also in number 4/3 or 3/2, the plates unusually bare of spinelets between the large spines except at the edges; actinal plates unusually elongate, partially overlying the abradial ends of the adambulacrals; adambulacral plates mostly with three spines in line at right angles to the furrow but in larger specimens, R > 70 mm, *c.* 10–15 proximal plates may have a fourth spine enlarged proximal to the abradial one; pedicellariae bivalved throughout, often very abundant, especially on the paxillae (Fig. 3j) where they are relatively short and rounded, their edges almost fully contiguous, actinal pedicellariae longer, sometimes broadened at the tips, numbering up to three on some proximal actinal plates, similar ones on the inferomarginals and oral plates while one to three more spiniform pedicellariae also occur on the furrow face of each oral plate near the mouth. Colour in life dark chocolate brown above except for a white band along the upper edge of each arm (possibly the superomarginals), the inferomarginal spines white with brown bases.

STATUS OF *L. barimae*. *Luidia barimae* was established on the basis of two poorly preserved specimens from off Venezuela. Walenkamp (1976) has recorded nine others from Surinam, evidently also in poor condition. About 50 further specimens from the *Pillsbury* collections off the north coast of South America have now been studied, as well as more than 100 from West Africa of *L. heterozona*. Though many of these are also poor, some are good enough to show that there are two matching regular longitudinal series of lateral paxillae adjacent to the superomarginal paxillae in the american and well as african specimens. Also the superomarginal paxillae are similarly markedly larger than the other paxillae (Fig. 2f). This leaves only the number of inferomarginal spines as a possible distinction between the two, *L. barimae* being described as having four spines proximally, then three, whereas no more than three, more often three and two, are said to be found in *L. heterozona* by Fisher, Madsen and Cadenat. However, one large *Pillsbury* specimen from the Gulf of Guinea, West Africa, with R at least 150 mm, was found to have four inferomarginal spines on a few proximal alternate plates, while conversely a specimen from Venezuela with R *c.* 120 mm has no more than three spines, though these reduce to two on the alternate distal plates. Certainly there is no justification for more than a subspecific distinction between specimens from the two sides of the tropical Atlantic and the minor difference in the marginal spines is clearly correlated with different growth rates.

DISTRIBUTION. *L. heterozona heterozona* from Cap Blanc, Mauritania, south to Elephant Bay, Angola; 28–975 metres. As noted above (p. 163), apart from Sibuet's Walda Expedition record (1975), the greatest depth recorded is 400 metres.

L. heterozona barimae from off the Gulf of Maracaibo, western Venezuela (*c.* 12°34′ N : 71°10′ W) eastwards to French Guiana (06°07′ N : 52°19′ W); 38–90 (?100) metres.

Luidia ludwigi scotti Bell
Figs 2a, e, 3t, u

Luidia scotti Bell, 1917 : 8–9; A. M. Clark, 1953 : 383–385, fig. 3, pl. 40, fig. 1; John & A. M. Clark, 1954 : 144; Carrera-Rodriguez & Tommasi, 1977 : 62, 65–66.
Luidia doello-juradoi Bernasconi, 1941 : 117; 1943 : 8–11, pl. 1, fig. 3, pl. 2, figs 2, 3, pl. 3, figs 4, 5.
Luidia rosaurae John & A. M. Clark, 1954 : 142–145, figs 1, 2, pl. 6, fig. 1; Jangoux, 1978 : 95.
Luidia ludwigi: Walenkamp, 1976 : 32–37, fig 9, pl. 2, figs 1, 2, 4, pl. 4, fig. 3.

R up to 90 mm; R/r 5·3–8·1/1, mean of 9 specimens 7·0/1.

A species of *Luidia* with normally 5 arms: abactinal paxillae with two longitudinal rectangular or squarish lateral series each side, matching each other and also the adjacent slightly smaller superomarginal paxillae, central paxillar spinelets distinctly coarser than the peripheral ones and in smaller specimens, R<*c*. 40 mm, where the median paxillae often have only a single central spinelet, this may stand out from the surface slightly but not as much as in *L. sagamina*; larger specimens with multiple central spinelets have them relatively shorter and making a uniform surface; inferomarginal plates mainly ventral in alignment, bearing one or two (in the largest specimens, R *c*. 90 mm, sometimes three) stout ambital spines, the upper one more or less shorter than the lower when there are two, on the ventral side 4 or 5 much smaller, almost cylindrical, but slightly tapering spines; adambulacral plates with 4 large spines, the abradial two in line parallel to the furrow; pedicellariae 3- or 4-valved on at least the more proximal actinal plates, the valves varying in shape from broadly spatulate to evenly tapering and triangular (see Fig. 3t, u), sometimes bivalved pedicellariae present on the paxillae and inferomarginal plates, absent from the furrow face of the oral plates. Colour (recently dried) patterned above with dark rose-coloured patches on the centre of the disc and bands across the arms, sometimes linked by continuous colour midradially.

SYNONYMY. The poorly-preserved holotype and two paratypes of *Luidia rosaurae* John & Clark, 1954, from off Venezuela, were thought to differ from *L. scotti* Bell, 1917, of southern Brazil in having only a single large ambital inferomarginal spine, finer ventral armament and more numerous pedicellariae. Walenkamp's material from Surinam (1976) and a number of *Pillsbury* and *Gerda* specimens from northern South America and the Florida Strait now studied, show that there is considerable variation in the development of the second (upper) inferomarginal spine, the thickness of the ventral spines and the frequency of the pedicellariae; consequently *L. rosaurae* cannot be maintained as specifically distinct. Walenkamp deferred a decision on this point in default of material from the type locality of *L. scotti*. Simultaneously, he rejected the synonymizing of *Luidia doellojuradoi* Bernasconi, 1941 with *L. scotti*, proposed by A. M. Clark (1953), on the grounds that its marginal paxillae are larger than the lateral ones and the R/r ratio is only 7/1. However, he was misled in this by Bernasconi's peculiar terminology of the lateral and superomarginal paxillae (see p. 166), the true superomarginal paxillae of *L. doellojuradoi* being in fact smaller than the lateral ones. Also in the 15 *Terra Nova* specimens of *L. scotti* the R/r ratio ranges upwards from 7/1; in the lectotype (incorrectly called holotype in 1953) it is 7·5/1. Thanks to Dr Bernasconi, there are two specimens which she named as *L. doellojuradoi* in the British Museum collections. Apart from the greater extent of the actinal pedicellariae on the arms and the occurrence of some inferomarginal pedicellariae—characters not considered to be of specific weight—no significant differences from *L. scotti* are apparent. The ventral armament of the inferomarginal plates has become appressed during preservation, which lends a rather coarser appearance than is shown by the well preserved type material of *L. scotti*.

It is also possible that *L. patriae* Bernasconi will prove to be synonymous with *scotti*.

Walenkamp (1976) percipiently noted the close affinity between *L. ludwigi* Fisher, 1906, from California and specimens from the north coast of South America conspecific with *L. rosaurae*, referring the latter to the synonymy of *L. ludwigi*. Fisher's holotype has R 110–115 mm and superficially resembles the larger Atlantic specimens seen except that it is rather coarser. A paratype of *L. ludwigi* with R 72 mm compares closely with a paralectotype of *L. scotti* of almost the same size but there appears to be a significant difference in the number of paxillar spinelets, the median paxillae of *ludwigi* rarely having less than 6 coarse ones whereas in *L. scotti* the number is most often only about 3. Possibly there is also a colour difference, Fisher having described *L. ludwigi* (at least when freshly preserved) as being reddish above 'sometimes mottled with lighter', whereas Atlantic specimens seem to be more boldly patterned dark (?red) and light. In conjunction with the geographical difference, these small differences are now considered to warrant a subspecific distinction.

One further nomenclatural threat still remains. Döderlein (1920), in listing *L. ludwigi*, noted that it is possibly (vielleicht) a synonym of *L. armata* Ludwig, 1905, from the Gulf of Panama. Accordingly, one of the two intact syntypes of *L. armata* from the U.S. National Museum has been studied; it has R 47 mm and is slightly decalcified and flaccid. The armament of the paxillae is more or less appressed, emphasizing the spiniform shape of the central spinelets. Although the larger Pacific specimens of *L. ludwigi* have markedly coarser and shorter central spinelets, tending to appear granuliform, smaller Atlantic specimens from the vicinity of Florida with R *c.* 40 mm, have a very similar relatively elongate armament and also agree in the shape and arrangement of the paxillae, plates and spines. However, the syntype of *L. armata* differs in having a very large, highly modified bivalved pedicellaria on each oral plate—a feature somehow overlooked by Ludwig and not found in the type material of *L. ludwigi* seen or any Atlantic specimens. It also has relatively small actinal interradial areas with no sign of a second row of actinal plates. At R 40 mm, *L. scotti* already has a single median interradial actinal plate distal to the main series and in larger specimens, R 50–60 mm, there are one or two such plates each side of the interradius. These two characters, but particularly the first, indicate that there are two distinct species in the East Pacific.

Distribution. Eastern Gulf of Mexico west of Florida, (*c.* 27½° N : 84° W) and Florida Strait, also the northern and eastern coasts of South America from Venezuela to northern Argentina (*c.* 39° S); 33–126 (?135) metres. The northernmost record from 85 miles west of St.Petersburg, Florida, is thanks to Dr. K. Serafy and with seven *Gerda* stations in the Florida Strait provides a considerable extension of the range from South America. About 35 specimens from 12 *Pillsbury* stations came from Venezuela to French Guiana and also served to extend the bathymetric range both up and down, the three shallowest—33, 36 and 42 metres—being from Surinam and French Guiana. There is also a specimen labelled as being from *Pillsbury* st. 1384, which is in the Puerto Rico Trench (*c.* 19°45′ N : 67°00′ W) at 7956 metres! Although it has relatively long arms (R/r 65/8 mm = 8·1/1), about the maximum found in *scotti*, the paxillar structure, form of the pedicellariae, general armament and banded colour pattern leave no doubt of the identification, but the locality is evidently a mistake.

Ludia patriae Bernasconi

Luidia patriae Bernasconi, 1941 : 117–118; 1943 : 11–13, pl. 1, figs 1, 2.

R 72 mm (holotype); R/r 7·2/1.

A species of *Luidia* with normally 5 arms; abactinal paxillae with the two lateralmost series forming transverse rows with the matching superomarginal paxillae and all rectangular or squarish in shape: inferomarginal plates mainly ventral in alignment, bearing two slightly flattened and slightly curved large spines near their upper ends at the ambitus, the lower one larger, and on the ventral side about six pointed spines, cylindrical or somewhat flattened; adambulacral plates with four large spines, the two abradial ones in line parallel to the furrow: pedicellariae absent throughout. Colour (dried) dark rose above with darker areas in the centre of the disc and on the median parts of the arms.

Affinities. *L. patriae* is very similar to *L. ludwigi scotti*, of which Bernasconi had as many as 80 specimens (as *L. doello-juradoi*), though only six or seven of *L. patriae,* which she supposed to differ in the absence of pedicellariae (not now thought to be a character of specific weight), the form, number and arrangement of the ventral inferomarginal spines and in lacking the two or three enlarged spinelets abradial to the four main adambulacral spines described for *L. doello-juradoi*. Possibly *L. patriae* will also prove to be a synonym of *L. ludwigi scotti.*

Distribution. Northern Argentina. 34½–37½° S [?also from Uruguay, 33°S]; 100–126 metres.

Luidia sagamina aciculata Mortensen

Fig. 1d, 2k, 3l, s

?Luidia alternata bicolor Verrill, 1915 : 203, pl. 12, fig. 1.
Luidia sagamina: Downey, 1973 : 24.
Luidia aciculata Mortensen, 1933*b* : 425–426, fig 7, pl. 20, figs 7–12; Fisher, 1940 : 268–269, fig. M5; Nataf & Cherbonnier, 1973 : 80–82, pl. 3, figs A, B, pl. 6, figs 1–6, pl. 9, figs G, H: Sibuet, 1975 : 284, 288.
Luidia sagamina var. *aciculata*: Madsen, 1950 : 199–203, figs 6, 7.
Luidia sagamina aciculata: A. M. Clark, 1955 : 33; A. M. Clark & Courtman-Stock, 1976 : 23, 32, 45.
Luidia atlantidea: Downey, 1973 : 25 [Non *L. atlantidea* Madsen, 1950.]

R up to 140 mm; R/r 7·0–10·5/1.

A species of *Luidia* with normally 5 arms; abactinal paxillae all with an enlarged median spinelet (sometimes replaced by a pedicellaria) both stouter and longer than the remaining spinelets; two (or in the largest specimens three) longitudinal series of lateral paxillae also matching transversely but outnumbering the much longer superomarginal paxillae by 16–19/10; inferomarginal plates mainly lateral in alignment, bearing two or three, sometimes four large spines, tending to alternate in number and position on consecutive plates, the uppermost spine the longest and projecting vertically upwards in its natural position, at least on every second plate; adambulacral plates with two or three large spines in a line at right angles to the furrow, when only two, the abradial one is relatively large; pedicellariae usually present on at least the proximal actinal plates, where they are more or less broadened basally and tapering so that the individual valves are triangular, though not closely contiguous except terminally, abactinal pedicellariae bivalved and shorter, sometimes absent but one or more elongate bivalved pedicellariae always present on the furrow face of each oral plate near the mouth, though not fully developed from spinelets in small specimens. Colour in life purple to purple-brown above, white below, marginal spines dark brown basally.

SYNONYMY. Madsen (1950) decided that *Luidia sagamina* Döderlein, 1920 from Japan and *L. aciculata* Mortensen, 1933 from St Helena are conspecific, following comparison of Mortensen's type material with a specimen from Sagami Bay and others collected off West Africa by the *Atlantide*. Although he retained *aciculata* as a subspecies, he could not find any real difference between it and *sagamina*. This prompted Downey (1973) to drop *aciculata* and use *L. sagamina* for some american specimens, though conversely Nataf and Cherbonnier in the same year retained *aciculata* at the specific level, without explanation. Madsen had also referred to *L. sagamina aciculata* a specimen from Durban, Natal and in 1976 (Clark & Courtman-Stock) I retained this terminology, though without having seen any specimens from either Japan or Natal. Since then, further echinoderm material from off Natal (A. M. Clark, 1977) has shown that the fauna of SE Africa has much in common with that of southern Japan and the East Indian area. This would imply that the Durban specimen should be named *L. sagamina sagamina* if two subspecies are to be recognized, as seems desirable to me in the absence of precedent from related species of moderate depths common to similar areas of the Atlantic and Indo-West Pacific.

A further complication is raised by the possibility that *Luidia sagamina aciculata* is conspecific with the (two?) specimens from the Florida Strait which Verrill (1915) called *Luidia alternata* variety *bicolor*. Verrill's drawings show relatively small single spines (or enlarged spinelets) on *all* the abactinal paxillae, quite different from the sporadic and much larger spines of *L. alternata*. Also the lateral paxillae outnumber the inferomarginal plates (the superomarginals were not distinguished by the artist) and the inferomarginal spines are regularly alternating on consecutive plates, as in *L. sagamina* and *aciculata*. Downey (1973) recorded a small specimen (R in fact 21 mm not 8 mm as given in her paper) from South Carolina as *L. sagamina* and mentioned another (p. 25) which she referred to *L. atlantidea* because of light lateral bands along the arms but which also proves to be conspecific with the first. A further specimen, R 24 mm, from *Gerda* st. 1039 in the Florida Strait may be

Halpern's supposed *L. atlantidea*, mentioned by Downey. Unfortunately the Bahama Expedition's specimens of *L. alternata* var. *bicolor* cannot now be found at the University of Iowa. Since the revival of *bicolor* as a specific name would mean that both *L. sagamina sagamina* and *aciculata* became junior synonyms and there is an element of doubt about the identity, it is desirable that the name *bicolor* should be formally set aside.

Verrill's specimens evidently had only two adambulacral spines, which is also the case in the small *Silver Bay* and *Gerda* specimens. Mortensen's holotype of *L. aciculata* from St. Helena, Fisher's *Discovery* specimen from off the Congo (Zaire), a *Pillsbury* specimen from the Gulf of Guinea (Fig. 2k) and an *Atlantide* west african specimen all usually have three adambulacral spines. Unfortunately, Madsen recorded four other *Atlantide* specimens with only two such spines and this is also true of two other *Pillsbury* Guinea specimens. Clearly, this character of adambulacral armament cannot be used to distinguish yet another american, as opposed to african, subspecies, comparable to the subspecies of *L. heterozona* and *L. alternata*, which would make for consistency of taxonomic treatment. The present american specimens are too small and too few to suggest other possible differential characters.

DISTRIBUTION. North Carolina to south and west Florida and from Cap Blanc, Mauritania south to Zaire and from St. Helena, 20–975 metres. As noted above (p. 163), apart from Sibuet's Walda Expedition record (1975), the greatest depth recorded is 150 metres.

Luidia sarsi Düben & Koren

Figs 1c, 2c, g, 3m–o, v, 6

Asterias sp. aff. *A. aranciaca*: M. Sars, 1835 : 39.
Luidia fragilissima (pt, five-armed specimens) Forbes, 1841 : 135–140.
Luidia Sarsii Düben & Koren, 1845 : 113; Perrier, 1875 : 342 [1876 : 262]; Sladen, 1889: 258; Süssbach & Breckner, 1911 : 210.
Luydia Savignyi (pt) Düben & Koren, 1846 : 254, pl. 8, figs 23, 24.
Luidia elegans Perrier, 1875 : 336–337 [1876 : 256]; 1884 : 269[?], pl. 10, fig. 7 [and probably also fig. 8], captioned '*L. barbadensis*'; Verrill, 1885 : 543, pl. 13, fig. 39; 1915 : 203–205, pl. 16, figs 4, 4a, pl. 19, fig. 1; Döderlein, 1920 : 289–290, fig. 36; Gray, Downey & Cerame-Vivas, 1968 : 140, fig 9; Downey, 1973 : 25, pl. 3, figs C, D; Blake, 1973 : 40–41, pl. 10, figs 27–52; Carrera-Rodriguez & Tommasi, 1977 : 71–75, figs 10–12.
Astrella simplex Perrier, 1882 : 21, fig. 25; 1894 : 193–194, pl. 14 , fig. 3.
Luidia africana Sladen, 1889 : 256–258, pl. 44, figs 1, 2, pl. 45, figs 1, 2; Koehler, 1923 : 132; H. L. Clark. 1923 : 252; 1925(pt) : 8; Mortensen, 1933*a* : 239–240, figs 3, 4; Madsen, 1950(pt) : 188–192, fig. 4, pl. 16, figs 3, 4; A. M. Clark, 1952 : 195; 1953 : 393–394, figs 10, 11; Nataf & Cherbonnier, 1973 : 79, pl. 8; A. M. Clark & Courtman-Stock, 1976 : 23, 30, 44, fig. 26. [Non *L. africana*: Koehler, 1911 : 19; Döderlein, 1920 : 228, nec Mortensen, 1925 : 178 = *L. atlantidea*.]
Luidia sarsi: Bell, 1893 : 72; Koehler, 1895 : 320, pl. 9. figs 6, 7; Ludwig, 1897 : 85–104, pl. 4, figs 2, 3, pl. 7, figs 1–12; Koehler, 1909 : 59; Döderlein, 1920 : 288–289, fig. 35; Koehler, 1921 : 57, fig.; Mortensen, 1925 : 178 [?*sarsi* acc. Madsen, 1950]; 1927 : 69, fig. 39b; Tattersall & Sheppard, 1934 : 36–55 (larvae); Madsen, 1950 : 187; Tortonese, 1965 : 150–152, fig. 69. [Non *L. sarsi*: Studer, 1884, = *L. africana* acc. Döderlein, 1920 but much more likely = *L. atlantidea*.]
Luidia paucispina von Marenzeller, 1893 : 3–4, pl. 1, fig. 1.

SIZE. The maximum size varies in different parts of the range. In NE Atlantic specimens (*L. sarsi sarsi*) R reaches only *c.* 110 mm (BM coll., W of Scotland) but the same subspecies from the Mediterranean, *L. sarsi africana* from South Africa and *L. sarsi elegans* from America may reach 180–190 mm R; R/r 5·0–10·5/1, usually 7·5–10·0/1 at R>90 mm.

DIAGNOSIS. A species of *Luidia* with normally 5 arms, becoming long and evenly tapering in large specimens, R>90 mm, but somewhat petaloid in smaller ones; abactinal paxillae relatively small and rounded, with two matching slightly coarser longitudinal lateral series each side but these are inconspicuous, outnumbering the markedly elongate superomarginal paxillae by 17–20/10, paxillar armament of fine spinelets of fairly uniform length, median paxillae mostly with only a single central spinelet, sometimes distinctly coarser in *L.*

sarsi sarsi where the peripheral spinelets are also less attenuated than in *L. sarsi africana* and *L. sarsi elegans* (see Fig. 3m, n, o); inferomarginal plates mainly lateral in alignment, bearing 2–4 usually 3, large pointed spines, showing some tendency to alternate in position and number on successive plates, the two upper spines similar in length, the uppermost often longer when not at its highest position; actinal plates distinctly broadened and keeled transverse to the arm axis; adambulacral plates with three large spines in series transverse to the furrow and sometimes one (or two) enlarged spinelets proximal to the lateralmost; pedicellariae bivalved with fairly broad rounded tips, usually almost circular in cross section but the valves sometimes rather flattened towards the tips, common on the median abactinal paxillae of *L. sarsi africana* and *L. sarsi elegans*, occasional in *L. sarsi sarsi* but longer actinal pedicellariae usually present in all three subspecies proximally, with one on the furrow face of each oral plate (exceptionally represented by two hardly modified spines). Colour in life brownish yellow, reddish or orange above, pale below, arms medially and marginal plates darker, especially in *L. sarsi africana*.

STATUS OF *L. africana* AND *L. elegans*. These two taxa of Sladen, 1889 and Perrier, 1875 are here regarded as conspecific with *L. sarsi*.

Confusion in the limits between *L. sarsi* and *L. africana* has arisen because the type material of the latter included one specimen from Atlantic Morocco besides the main sample from South Africa, one of the latter conforming to the size and description given by Sladen, as I noted in 1953 (p. 393). The moroccan specimen has fairly numerous globose pedicellariae on the abactinal paxillae, as in the southern specimens. Although such pedicellariae were thought to be rare in north european specimens of *L.*. *sarsi*, some larger specimens from west of Scotland collected since 1953 were found to have more or less numerous pedicellariae (Fig. 3m), sometimes two or three on a single paxilla. It is significant that there are no reliable identifications of *L. africana* from any localities between Cape Verde and Luderitz Bay, Namibia. Despite a critical comparison by Nataf & Cherbonnier (1973) out of 213 five-armed specimens of the *ciliaris*-group (excluding *L. sagamina aciculata*) from this area, every one was found to be referable to *L. atlantidea* and not to *L. africana*. Döderlein's record (1920) of *L. africana* from the Cape Verde Islands (based on two specimens named *L. sarsi* by Studer in 1884) is clearly in mistake for *L. atlantidea* since he particularly notes the relative coarseness of the central paxillar spinelets and the occurrence of pedicellariae on the superomarginal but not the abactinal paxillae—the reverse of what is found in *L. africana*, where both central and peripheral paxillar spinelets are uniformly fine. Madsen (1950) has referred Mortensen's larger moroccan specimens also to *L. atlantidea*, leaving under the heading of *L. africana* only some smaller moroccan ones which 'might just as well belong to *L. sarsi*' and three fragmentary *Atlantide* specimens which 'are not immediately recognizable as *L. africana*'. Zoogeographically, it would be expected that the distribution of a northern species also found in the Mediterranean, could well extend southwards to some extent in north-west Africa, as with *Marthasterias glacialis*, for instance, which also occurs in South Africa but is unrecorded between Cape Verde and Cape Town.

There are in the British Museum collections six specimens from near Cap Blanc (*Discovery* stations 8005 and 8020, 101 and 261–297 metres) with R 32 to *c.* 140 mm. These are certainly not *L. atlantidea*, having uniformly fine paxillar armament, abactinal rather than superomarginal pedicellariae, no white lines emphasizing the positions of the superomarginals but darker brown midlines to the arms, much as in *L. sarsi* and *L. africana*. These specimens are a little unusual in having the pair of lateral spines on the furrow face of each oral plate hardly modified, if at all, into a pedicellaria. One exception is the smallest one, surprisingly since it is usually in larger specimens of species such as *L. heterozona* that this pedicellaria is more modified. Nearly all the specimens of *L. sarsi, africana* and *elegans* seen have quite a well-developed oral furrow pedicellaria, though the two spines from which it is modified may be more or less unequal in size. A second feature of some of these Cap Blanc specimens is that some proximal superomarginal paxillae are unusually broad, almost square, rather than consistently elongated, squarish paxillae being a characteristic of *L.*

atlantidea. This is naturally limited to the plates adjacent to those inferomarginals where the highest spine is not at the upper edge of the plate.

In describing *L. africana*, Sladen (1889) cited seven supposed differences from *L. sarsi*, the larger size (R up to 160 mm in the type material), the more even taper of the arms, the smaller size of the median paxillae, the lesser prominence of the central median paxillar 'granule' (spinelet), the greater length of the uppermost inferomarginal spine relative to the second spine, the greater length of the third (lateralmost) adambulacral spine, achieving equality with the second spine, and the less pointed form of the actinal pedicellariae. Subsequently Madsen (1950) noted that abactinal pedicellariae are not only much more often found in *L. africana* than in *sarsi*, where they are rare, but also that their position, when present in *sarsi*, is peripheral, while those of *africana* are central on the paxillar tabulum, so that the pedicellariae of *sarsi* tend to be seen in profile rather than from the top. He also noted that the inferomarginal spines of *L. africana* differ in having dark pigmented skin basally.

As far as size is concerned, although in Norway, the type locality of *L. sarsi*, larger specimens usually have R only 50–60 mm, around Scotland it may reach *c.* 110 mm and in the Mediterranean reputedly *c.* 180 mm (diameter 35 cm). Such larger specimens also have the arms more attenuated and evenly tapering and there is greater disparity in the size of the additional median paxillae. As for the relative lengths of the inferomarginal and adambulacral spines, these are dependent to some extent on growth, the lateralmost adambulacral spine being retarded in growth relative to the second spine, while it would be more correct to say that the two upper inferomarginal spines of *L. sarsi* are similar in length, the uppermost one often slightly longer, especially on those plates where it is not in its highest position, as is the case in the lectotype now proposed (see below), even though R is less than 40 mm. At R 100+ mm the third spine approximates in length to the other two in specimens from all localities, a characteristic thought by Döderlein (1920) to be diagnostic of *L. elegans*.

With regard to the occurrence of abactinal pedicellariae, in 1953 I noted that in four out of ten northern specimens of *L. sarsi* studied, some pedicellariae were present. As mentioned above, subsequent scottish collecting has yielded material with pedicellariae as numerous as in the moroccan paratype of *L. africana* and some south african specimens. In 1953 I also contended that the pedicellariae are not really central on the paxillae of *L. africana* (or *L. elegans*) either but that this may appear so when the paxillae are crowded in preservation and the valves are coarser, pushing the pedicellariae into a more nearly vertical alignment on the tabulum. There is rarely a complete circlet of spinelets, as shown in Mortensen's fig. 3 (1933*a*) and Madsen's fig. 4c, d (1950). The shape of the pedicellariae, both abactinal and actinal ones, varies to some extent in different specimens from both north and south. Viewed end-on, the outline is usually approximately circular and the shape appears globular but may be slightly oval in one plane or the other if the valves are either thickened or broadened. The very broad shapes of both kinds of pedicellaria shown in Madsen's fig. 4h, i and k (1950), the abactinal ones cockle-shaped and the actinal ones with the individual valves bat-shaped (fan-shaped according to Madsen) seems to be exceptional even among south african specimens, none of the ten now studied having such an exaggerated form. Usually their actinal pedicellariae are either tapered in both side views (like a bishop's mitre) or else the tips are blunter and often thicker, a range also shown by northern specimens.

Finally, the shape of the abactinal paxillar spinelets needs to be compared. In many northern specimens of *L. sarsi* the majority of median paxillae do have the single central spinelet distinctly coarser than the peripheral ones, appearing almost granuliform as foreshortened. This is particularly, but not exclusively, true of smaller specimens, including the lectotype, but in other specimens the thickness of all the paxillar spinelets is similar. A comparable modification of the central paxillar spinelet is noted above in some smaller specimens of *L. ludwigi scotti* and of course in a much more exaggerated form in *L. sagamina aciculata*, where the central spinelet is more or less markedly elongated as well as being much thicker than the peripheral spinelets. In general, the paxillar spinelets of south african specimens are appreciably more attenuated than those of european specimens and none have been observed to show a coarsening of the central spinelet, though it should be emphasized that no specimens with $R < 70$ mm are available.

To sum up, in comparison between specimens from South Africa and those from Europe and NW Africa, no differences of specific weight can be found. There are slight differences in the armament of the paxillae in some specimens, the southern ones tending to have a finer and more uniform armament but this seems to be shared by some moroccan specimens and is always very subtle. Although the frequency of pedicellariae seems to increase further south, only in occasional south african specimens with extremely broad pedicellariae are these organs distinctive. It is therefore doubtful whether the name *africana* is worth retaining for a subspecies from South Africa but the distribution gap in west Africa coupled with these minor morphological differences may justify it.

With regard to *Luidia elegans* from the american side of the Atlantic, the only comparison given by Perrier was of the ventral side with that of *L. alternata* just described, the difference emphasized being the bivalved rather than trivalved pedicellariae. In Döderlein's key (1920), he distinguished *L. elegans* from the much more closely related *L. sarsi* and *L. africana* by the equal length of all three inferomarginal spines being supposedly limited to *L. elegans*, which was also said to be the only one to have numerous paxillar pedicellariae. This comparison was evidently made primarily on the evidence of a single small specimen of *L. sarsi* (R 29 mm), one of *L. elegans* with R 145 mm and two specimens from the Cape Verde Islands which he thought to be *L. africana* but are more likely *L. atlantidea*. Inevitably, in smaller specimens the lowest inferomarginal spine, if developed at all, is relatively smaller, while at most stages of growth the two upper spines are similar in length, as discussed above. At R *c.* 100 mm in European specimens all three spines may be about equal, while the occurrence of pedicellariae is clearly variable and of little taxonomic weight.

However, there does appear to be a significant difference in the number of abactinal paxillae across the arm, at least in smaller specimens, R 40–50 mm, on the two sides of the Atlantic. Excluding the two series of superomarginal paxillae, the number in american specimens of about this size is proximally *c.* 13 compared with *c.* 17 in those from the East Atlantic. Unfortunately, owing to their irregular arrangement, it is difficult to make a precise estimate of the number of paxillae, especially in larger specimens. Also, the limited amount of material available indicates that the paxillar number may increase at a higher rate in american specimens. There is a small degree of support for this character in the armament of the adambulacral plates. At R *c.* 40 mm, the third (lateralmost) spine is much smaller than the second in american specimens and even at R 70 mm this spine is still much narrower basally than the second and only about two-thirds as long. Only when R approaches 140 mm does the third spine achieve parity in magnitude with the second on most plates. As for the accessory adambulacral spinelets, in specimens from both sides of the Atlantic one (sometimes two) is usually somewhat enlarged proximal to the third spine (or the space between second and third spines). This spinelet is usually one-third to half, but occasionally as much as three-quarters as long as the third spine. In american specimens this accessory spinelet(s) remains slender but in the eastern Atlantic can be basally stouter and more conical in shape. However, there is so much variation in the adambulacral armament that these differences cannot be of much importance. Finally, the madreporite may remain obscured by the paxillae to a greater extent in specimens from the eastern Atlantic than in american ones but this is probably correlated with size (the plate becoming more prominent in larger specimens) and is affected by preservation. In total, these minor differences do not add up to more than a subspecific distinction between *L. elegans* and *L. sarsi*.

Finally, Koehler (1923) and Carrera-Rodriguez & Tommasi (1977) have recorded specimens from Uruguay (33° S) and southern Brazil (*c.* 30½° S) as *L. africana* or *L. elegans*. Because of the great geographical discontinuity between them and the rest, comparable to that between *L. sarsi sarsi* and *L. sarsi africana*, it is not improbable that a minor morphological difference justifying a taxonomic distinction of eastern south american specimens may exist, most likely again at the subspecific level.

Lectotype. Because of the complex affinities of *Luidia sarsi*, it seemed desirable that a lectotype be selected from among Sars' material from Bergen to which Düben & Koren gave this name in 1845. Thanks to Dr M. E. Christiansen of the Zoologisk Museum, Oslo, it is clear that no type was designated at the time. The specimen chosen (one of seven) was from Manger, near Bergen, Oslo Museum reg. no. E1005a, shown in Fig. 6.

R (maximum)/r is 37/8 mm, = 4·6/1. The shorter arms have R 30 and 32 mm. (The relatively low R/r ratio is to be expected at this relatively small size.) About 17 lateral paxillae correspond to 10 of the more proximal superomarginal paxillae. The median paxillae nearly all have a single, slightly coarser, central paxillar spinelet and usually 7–11 peripheral spinelets. Excluding the superomarginal ones, there are *c.* 17 paxillae across the arm breadth basally. The paxillae of the outer lateral row have up to three central spinelets.

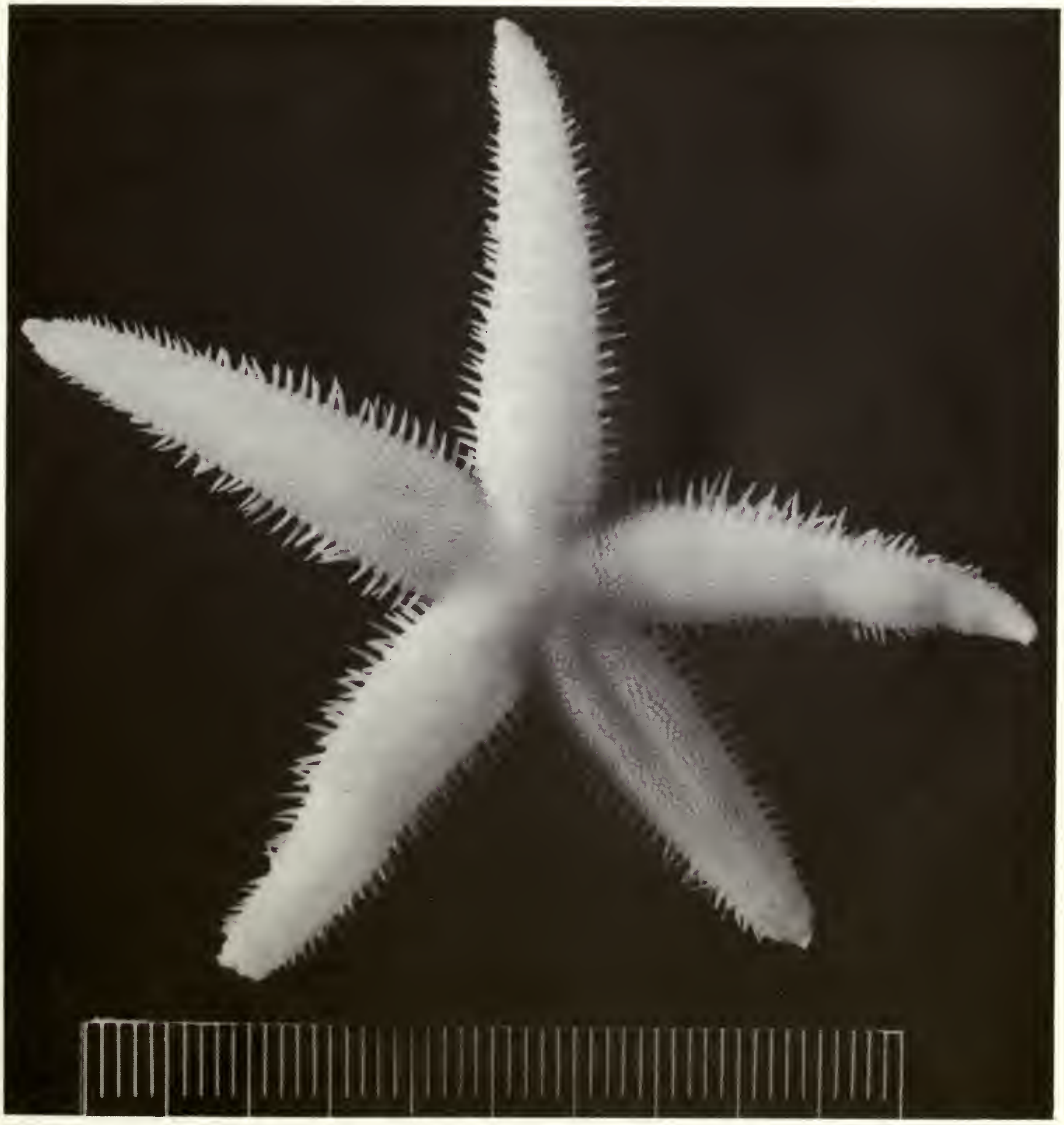

Fig. 6 *Luidia sarsi sarsi* Düben & Koren, lectotype, Zoologisk Museum, Oslo reg. no. E1005a, Manger, near Bergen. Dorsal view, × 2·2.

All the spinelets of the lateral paxillae are distinctly coarser than those of the median ones, while the superomarginal armament is coarser still. The madreporite is not distinguishable. The inferomarginal plates bear 2–4 large spines, rather variable in level on the plate, sometimes alternating, though at the same level on several consecutive plates. The uppermost spine is usually slightly the longest. Most proximal actinal plates bear a single blunt, bivalved pedicellaria but no abactinal pedicellariae were observed. Each adambulacral bears 3 large spines and an enlarged spinelet one-third to half as long as the lateralmost one and proximal to it. Each oral plate bears about four large spines in an abradial row and one other spine near the furrow margin, besides a large bivalved pedicellaria in the furrow.

The paralectotypes include four smaller specimens and two larger but broken ones, one with R *c.* 50 mm and the other R/r 55/9·5. The central spinelet of the median paxillae is also distinctly coarser than the peripheral ones; *c.* 20 lateral paxillae correspond to 10 superomarginal ones; proximally there are usually four inferomarginal spines.

HOLOTYPE OF *Luidia elegans*. Because of Perrier's rather inadequate description, this specimen was borrowed for reexamination from the Museum of Comparative Zoology, Harvard. The number is M.C.Z. 372. It proved to be in fact the specimen illustrated in Perrier, 1884, pl. 10, fig. 7, under the name of *L. barbadensis*, though the negative was reversed in printing. One arm is abnormally short, probably regenerated, and curled up at the tip. R is *c.* 40 mm for the longest arm (Perrier gives 35 mm); r is 7 mm; 18 lateral paxillae correspond to 10 superomarginal ones; proximally there are *c.* 13 paxillae across the arms between (but not counting) the superomarginal ones. The median paxillae mostly have only a single central spinelet, not at all coarser than the peripheral ones. No abactinal pedicellariae were seen. Most inferomarginal plates bear three large spines, sometimes two, showing a tendency for alternation in position. The actinal pedicellariae are bivalved and blunt-tipped. The third adambulacral spine is reduced on some plates. The locality is 'Straits of Florida, 101 fathoms'. Verrill's guess that Perrier's '101 brasses' meant *feet* being incorrect.

DISTRIBUTION. *L. sarsi sarsi* from Trondheim Fjord, Norway to Cap Blanc, Mauritania, the Azores and the Mediterranean; 9–1300 metres.

L. sarsi africana from Luderitz Bay to the Port Elizabeth area of South Africa; 54–360 metres.

L. sarsi elegans from east of New Jersey, U.S.A. (*c.* 41° N) to the Florida Strait and both east and west Gulf of Mexico; also from southern Brazil (*c.* 30½° S) to Uruguay (*c.* 33° S); 60–365 metres. There are no reliable records from the caribbean, Perrier's supposed specimens from Barbados being untraced in the M.C.Z. and it is significant that no specimens appear to have been taken by the intensive collections of the *Atlantis* around Cuba (H. L. Clark, 1941) or by the *Pillsbury* in the caribbean, Lesser Antilles or north of South America.

Luidia senegalensis (Lamarck)

Asterias senegalensis Lamarck, 1816 : 567.

Luidia senegalensis: Müller & Troschel, 1842 : 78, pl. 5, fig. 4; Perrier, 1875 : 342–343 [1876 : 262]; Döderlein, 1920 : 249–250, figs 9, 20; H. L. Clark, 1933 : 20–22; Bernasconi, 1943 : 5–6; Tommasi, 1958 : 9–11, pl. 2, fig. 2; Ummels, 1963 : 94–95, pls 10, 11; Downey, 1973 : 22, pl. 1, figs A, B; Blake, 1973 : 30, pl. 2, figs 1–31; Walenkamp, 1976 : 25–29, fig. 5, pl. 1, fig. 4; 1979 : 12, pl. 1, figs 1–3.

Luidia marcgravii Steenstrup *in* Lütken, 1859 : 43–46; Verrill, 1915 : 208–209; Boone, 1933 : 76, pls 33–36; Bernasconi, 1958 : 125–127.

REMARKS. A very large specimen from *Pillsbury* st. 750, off Venezuela, 22–26 metres with R up to 252 mm may provide a size record.

This locally common caribbean species with its numerous and particularly attenuated arms seems even more vulnerable than most Luidias to loss and regeneration of the arm tips, probably due to predation, possibly cannibalism.

Distribution. Sporadically in southern Florida and from Jamaica eastwards along the Antilles, also Belize and Nicaragua and along the north coast of South America to southern Brazil (Santa Caterina, *c.* 27° S); the original record from Senegal has never been repeated; the records from Belize and Nicaragua are new and derived from the *Pillsbury* collections; 1–64 metres, the depth range also being extended by a *Pillsbury* station (745, off Venezuela, *c.* 12° N, 67° W); the previous maximum depth was 45 m off French Guíana.

Summary of taxonomic changes

The number of nominal Atlantic species of *Luidia* is reduced by the present study from a one-time maximum of 17 to 11.

Luidia aciculata Mortensen, 1933*b* is retained as a subspecies of the Indo-West Pacific *L. sagamina* Döderlein, 1920.

L. africana Sladen, 1889 is reduced to a subspecies of *L. sarsi* Düben & Koren, 1845.

L. barimae John & Clark, 1954 is reduced to a subspecies of *L. heterozona* Fisher, 1940.

L. bernasconiae A. H. Clark, 1945 is again synonymized with *L. alternata* (Say, 1825), having been revived by Gray, Downey & Cerame-Vivas, 1968.

L. elegans Perrier, 1875 is reduced to a subspecies of *L. sarsi.*

L. numidica Koehler, 1911 is treated as a subspecies of *L. alternata.*

L. quequenensis Bernasconi, 1942 is synonymized with *L. alternata.*

L. rosaurae John & Clark, 1954 is synonymized with *L. scotti* Bell, 1917, which is treated as a subspecies of the East Pacific *L. ludwigi* Fisher, 1906.

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New and little known species of Oncaeidae (Cyclopoida) from the Northeastern Atlantic

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Introduction

A large number of new species and genera belonging to the Oncaeidae have been described in recent years. Many common species have been re-examined and recognized as polytypic, comprising two or more varieties (Tanaka, 1960; Moulton, 1973; Ferrari, 1975; Boxshall, 1977) or two or more species (Heron, 1977). Now that some of the better known species have been redescribed in greater detail it is obvious that many of the newly described species are also in need of more exact description. Taxonomic study of oncaeids has become a very laborious process, demanding the recognition of relatively small morphological differences in these microscopic animals, half the known species of which are less than 0·6 mm in body length.

Most records of oncaeids are from the epipelagic zone, but the more recent discovery of several species extending down into the deep bathypelagic zone (below 2000 m) indicates that previous records reflect the limitations of the sampling programmes rather than any true restrictions in their depth range.

A new species, *Oncaea heronae*, and two little known species belonging to the genus *Oncaea* are here described. The genera *Conaea, Epicalymma* and *Myctospictosum* are synonymized with *Oncaea*. New locality records are presented for six species and two previously undescribed males and two juveniles of known species are also described.

Materials and methods

The material described below was donated to the British Museum (Natural History) by the Institute of Oceanographic Sciences (Wormley) and the Marine Biological Association (Plymouth). It was collected in April 1977 at station 9541 (20° N 21° W) in the NE Atlantic during cruise 82 of the R.R.S. *Discovery*, and in September 1979 at the mouth of the English Channel (48° N 7°30′ W) during a cruise of the R.V. *Sarsia*. The *Discovery* material was collected by a 80 μ mesh diatom net attached to the RMT 1 + 8 net system. *Sarsia* material was taken using a pump system with 80 μ and 200 μ mesh filters.

Material was preserved in 10% sea water formalin, stained in chlorazol black, dissected in lactophenol and mounted in polyvinyl lactophenol. Drawings were made with the aid of a *camera lucida*. Specimens were measured using an eyepiece micrometer, total body length being the distance from the tip of the rostrum to the apex of the caudal rami.

Descriptions of species

Oncaea tregoubovi Shmeleva, 1968

O. tregoubovi Shmeleva, 1968 : 1784–1785, figs 1–12.

DESCRIPTION· *Female.* Ratio of prosome and urosome lengths 1·8 : 1. Prosome elongate, oval in dorsal aspect (Fig. 1a). Mean body length of 3 specimens 0·34 mm (range 0·31 to

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0·37 mm). Third prosome segment without a dorsal projection. Head (first prosome division) 1·3 times longer than wide. Proportional lengths of ursome and caudal rami 8 : 57 : 5 : 4 : 13 : 13 (Fig. 1b). Genital apparatus located on dorsal surface anterior to midpoint of genital segment; each area armed with a setule. Maximum width of genital segment at level of genital apparatus; length to width ratio 1·75 : 1. Caudal rami twice as long as wide.

First antenna 6-segmented (Fig. 1c); armature: I–2, II–7, III–3, IV–3, V–2, VI–5 (some elements may be missing); ratio of segment lengths 10 : 13 : 46 : 13 : 8 : 10. Second antenna 3-segmented (Fig. 1d); first segment bearing 1 long pinnate seta distally; second segment bearing a row of denticles along internal surface; terminal segment longer than second and bearing 5 curved spines and 2 curved setae. Mandible bearing 5 elements (Fig. 1e): a stout seta on external surface, 2 broad blades, 1 bearing a row of setules along internal edge, and the other unarmed, and 2 setae, 1 long and hirsute, the other small and unarmed. First maxilla bilobed (Fig. 1f); bearing 1 seta on internal surface; 2 setae on internal lobe and 2 setae, a setose seta and a spine on external lobe. Second maxilla 2-segmented (Fig. 1g); second segment produced distally as an elongate, curved, bilaterally spinulose claw; also having an external pinnate seta and an internal bilaterally spinulose element. Maxilliped 4-segmented (Fig. 1h); first segment unarmed; internal surface of second segment with 2 spines, distal spine bidentate; third segment reduced; terminal segment produced as a long claw and armed with a row of setules on concave surface, an internal basal spine and an external basal setule.

Endopodites and exopodites of natatory legs 3-segmented (Figs 2a–d); external spines of exopodites bilaterally serrate; armature of natatory legs as follows:

	Coxa	*Basis*	*Endopodite*	*Exopodite*
Leg 1	0–0	1–I	0–1; 0–1; 0, I, 5	I–0; I–1; III, I, 4
Leg 2	0–0	1–0	0–1; 0–2; II, I, 3	I–0; I*–1*; III, I, 5
Leg 3	0–0	1–0	0–1; 0–2; II, I, 2	I–0; I–1; II, I, 5
Leg 4	0–0	1–0	0–1; 0–2; II, I, 1	I–0; I–1; II, I, 5

* = segment missing from figured specimen (Fig. 2b), present in other material.

Terminal spines of exopodites longer than terminal segments bearing them but terminal spines of endopodites shorter than terminal segments; each terminal spine bordered by a serrate membrane unilaterally; endopodites of legs 1–3 terminate in conical projections; all setae on legs plumose. Fifth leg comprising a small cylindrical segment bearing a single terminal seta on body surface near leg (Fig. 1i).

MATERIAL EXAMINED. 3♀♀ from sample 9541.24, 2980–3560 m. 20° N 21° W. BM(NH) 1981.114.

REMARKS. This species was identified by the following combination of characters: the relative lengths of the segments of the first and second antennae, the armature of the maxilliped and natatory legs, and the relative dimensions of the urosome segments. Some minor differences were found between the present material and the original material figured by Shmeleva (1968). Most notably Shmeleva (1968 : Fig. 9) shows the fourth natatory leg with the internal margin of the third endopodite segment unarmed, whereas the present specimens have a single seta. The absence of this seta is atypical for *Oncaea* species. It may be significant that Shmeleva does not mention this character in the text of the description, and the original drawing may be inaccurate or based on a specimen with incomplete armature. This species has only been recorded once before, from the southern Adriatic where it was taken between 200 and 300 metres depth.

Oncaea ivlevi Shmeleva, 1966

O. ivlevi Shmeleva, 1966 : 932–933, Plate I, figs 1–11.

DESCRIPTION. *Female.* Ratio of prosome and urosome lengths 1·7 : 1 (Fig. 3a). Body length of 3 specimens 0·33 mm. Third prosome segment without a dorsal projection (Fig. 3b). Head

1·1 times longer than wide. Proportional lengths of urosome segments and caudal rami 8 : 50 : 7 : 6 : 18 : 11 (Fig. 3c). Genital apparatus situated anterior to midpoint of dorsal surface of genital segment; each area armed with a setule. Maximum width of genital segment at the level of genital apparatus; length to width ratio 2 : 1. Genital segment not markedly swollen. Caudal rami nearly twice as long as wide, curving outwards and each bearing a stout spine at external corner.

First antenna armature similar to *O. tregoubovi* (Fig. 3d); ratio of segment lengths 19 : 19 : 35 : 12 : 6 : 9. Second antenna armature similar to *O. tregoubovi* except that first segment armed with a row of setules on internal surface, and second segment with a row of spinules; terminal segment equal in length to second segment (Fig. 3e). Mandible and first maxilla lost during dissection. Second maxilla like that of *O. tregoubovi* (Fig. 3f). Maxilliped 4-segmented (Fig. 3g); first segment unarmed; internal surface of second segment with 2 spines, longer distal spine spinulose; second segment also bearing a row of denticles along internal surface; third segment reduced; terminal claw bearing a row of spinules along concave surface and an internal basal spine.

Armature of natatory legs similar to *O. tregoubovi* (Figs 3h–k), but terminal segment of second endopodite bearing 1 spine on external surface instead of 2; endopodites 2, 3 and 4 tipped with relatively small conical projections; terminal spines of exopodites 1 and 2 slightly longer than terminal segments; those of exopodites 3 and 4 slightly shorter; all terminal spines of endopodites shorter than terminal segments and bilaterally flanged. Fifth leg comprising a small cylindrical free segment bearing 2 setae, outer double length of inner; and a seta on body surface near the leg.

Male. Ratio of prosome and urosome lengths 1·6 : 1 (Fig 4a and b). Mean body length of 6 specimens 0·33 mm (range 0·28 to 0·35 mm). Head 1·1 times longer than wide. Proportional lengths of urosome segments and caudal rami 7 : 60 : 2 : 3 : 2 : 13 : 13. Genital lappets produced into small postero-lateral processes (Fig. 4c). Genital segment with length to width ratio 2·1 : 1. Caudal rami twice as long as wide, as in female possessing a stout spine on each ramus.

Mouthparts similar to those of female except first antenna and maxilliped. Three distal segments of the first antenna fused. Maxilliped 3-segmented (Fig. 4d); first segment unarmed; second segment bearing 2 short spines and a row of setules on internal surface; terminal claw bearing spinules on concave surface and a stout external basal spine. Legs 1–5 similar to those of female.

MATERIAL EXAMINED. 3♀♀ and 6♂♂ from sample F166–F170, 80–40 m, 48° N 7°30′ W. BM (NH) ♀♀ 1981.115–116, ♂♂ 1981.117–119 and 1981.124.

REMARKS. This species was identified by the following combination of characters: the armature of the natatory legs, the relative dimensions of the urosome segments, and the presence of the stout caudal spine. The present specimens differ from Shmeleva's descriptions in a few minor details: in the possession of 3 terminal setae in association with the spine on the caudal rami rather than 2, the possession of an extra row of spinules on both the distal spine of the second segment of the female maxilliped and the terminal claw. There are also small differences in the lengths of the terminal exopodite spines. This species has also been recorded from the southern Adriatic where it was taken between 50 and 100 metres depth (Shmeleva, 1966) and from the Atlantic at 15 stations from 9° S 25° W to 9° S 45° W between 10 and 2000 metres depth (Shmeleva, 1969).

Oncaea hispida (Heron, 1977) Comb. nov.

Conaea hispida Heron, 1977 : 90–95, Figs 33h–j, 34a–k.

DESCRIPTION. *Female.* Ratio of prosome and urosome lengths 1·75 : 1 (Fig. 5a). Body length of 1 specimen 0·56 mm. Third prosome segment without dorsal projection. Proportional lengths of urosome segments and caudal rami 8 : 48 : 7 : 7 : 18 : 12 (Fig. 5b). Genital apparatus located on dorsal surface anterior to midpoint of genital segment, each area armed with a setule. Maximum width of genital segment at level of genital apparatus; length to width ratio 1·6 : 1. Caudal rami 1·3 times as long as wide. Appendages similar to those described by Heron with only minor differences apparent (Figs 5c–h and 6a–d).

Male. Ratio of prosome and urosome lengths 2 : 1 (Fig. 6e). Body length of 1 specimen 0·55 mm. Head 1·2 times longer than wide. Proportional lengths of urosome segments and caudal rami 10 : 51 : 3 : 3 : 3 : 18 : 12 (Fig.. 6f). Genital lappets produced into small posterior processes. Genital segment with length to width ratio 1·5 : 1. Caudal rami approximately as long as wide.

Mouthparts similar to those of female except first antenna and maxilliped. The 3 distal segments of first antenna fused. Maxilliped 3-segmented (Fig. 6g); first segment unarmed; second segment bearing 2 rows of dentiform processes on internal surface; terminal claw unarmed. Legs 1–5 similar to those of female.

Fifth Copepodid (female). Ratio of prosome and urosome lengths 2 : 1 (Fig 6h). Body length of 1 specimen 0·46 mm. Head approximately as long as wide. Urosome 4-segmented (Fig. 6h). Proportional lengths of urosome segments and caudal rami 10 : 45 : 6 : 29 : 10. Genital segment without visible genital apparatus, length to width ratio 1·5 : 1. Caudal rami 1·2 times as long as wide. Appendages similar to those of adult female except that proximal seta on second segment of juvenile maxilliped is pinnate (Fig. 6j).

MATERIAL EXAMINED. 1♀, 1♂, 1♀ juvenile from sample 9541.24, 3980–3960 m, 20° N 21° W. BM(NH) 1981.120–122.

REMARKS. This species is here transferred from the genus *Conaea* to *Oncaea* (for discussion see page 191), and was identified by the following combination of characters: the length of the terminal segment of the second antenna and its armature, the armature of the maxilliped and the length of the third segment of the fourth endopodite. There are minor differences between the present material and Heron's description of the female in the ratio of urosome segment lengths, in the proximal spine of the second segment of the maxilliped which lacks the spinules in the adult female (but not in the juvenile), and the fifth leg has 2, rather than 1, tubercles each bearing at seta. These differences are considered to represent geographical variation within the species, as the only previous records of this species are from the antarctic zone of the southwest Pacific between 1000 and 2000 metres depth. The male and fifth copepodid have not previously been described.

Oncaea heronae sp. nov.

DESCRIPTION. *Female.* Ratio of prosome and urosome lengths 1·5 : 1. Prosome elongate and oval in dorsal aspect (Fig. 7a). Mean body length of 4 specimens 0·33 mm (range 0·31 to 0·35 mm). Third prosome segment without a dorsal projection. Head 1·1 times longer than wide. Proportional lengths of urosome segments and caudal rami 9 : 50 : 7 : 7 : 13 : 14 (Fig. 7b). Genital apparatus located on dorsal surface anterior to midpoint of genital segment. Maximum width of genital segment at level of genital apparatus; length to width ratio 1·2 : 1. Caudal rami twice as long as wide.

First antenna 6-segmented (Fig. 7c); armature: I–3, II–6, III–3, IV–1, V–2, VI–5 (some elements may be missing); ratio of segment lengths 12 : 22 : 34 : 13 : 7 : 12. Second antenna 3-segmented (Fig. 7d); first segment bearing 1 long pinnate seta distally; second segment unarmed; terminal segment equal to second segment in length, bearing 1 curved spine and 3 curved setae proximally and 5 curved spines and 1 curved seta distally. Mandible lost during dissection. First maxilla (Fig. 7e) and second maxilla (Fig. 7f) with armature similar to *O. tregoubovi.* Internal surface of second segment of maxilliped bearing 2 overlapping rows of setules and 2 spines; larger distal spine bilaterally dentate (Fig. 7g); terminal claw with smooth concave surface; single internal basal spine.

Armature of natatory legs similar to *O. tregoubovi* except for armature of terminal segments of endopodites 2–4:

	Coxa	*Basis*	*Endopodite*	*Exopodite*
Leg 1	0–0	1–I	0–1; 0–1; 0, I, 5	I–0; I–1; III, I, 4
Leg 2	0–0	?–0	0–1; 0–2; I, I, 3	I–0; I–1; III, I, 5
Leg 3	0–0	1–0	0–1; 0–2; 0, I, 2	I–0; I–1; II, I, 5
Leg 4	0–0	?–0	0–1; 0–2; 0, I, 1	I–0; I–1; II, I, 5

Bilaterally serrate spines on external margins of exopodites lack pronounced flanges (Figs 7h–k); first endopodite with conical terminal projection; all terminal spines shorter than terminal segments except terminal spines of fourth exopodite and endopodite, these being longer than terminal segments. Fifth leg comprising small free cylindrical segment bearing 2 terminal setae, the longer, internal seta extending to level of genital apertures.

Male. Not known.

MATERIAL EXAMINED. 4♀♀ from sample 9541.24, 3980–3960 m, 20° N 21° W. BM(NH) Holotype 1981.125, paratypes 1981.126.

ETYMOLOGY. This species has been named after Gayle A. Heron of the University of Washington, Seattle, in recognition of her work on the taxonomy of the Oncaeidae.

REMARKS. The second, third and fourth endopodites of *O. heronae, O. brodskii* Shmeleva, 1968 and *O. longipes* Shmeleva, 1968 have the same unusual armature described above, but *O. heronae* can be distinguished by other small differences in the armature of the natatory legs, by the 2 overlapping rows of setules on the second segment of the maxilliped, and by the structure of the free segment of the fifth leg which is elongate in *O. longpipes* and reduced to a tubercle in *O. brodskii*, but small and delimited from the body segment in *O. heronae.*

Oncaea setosa Heron, 1977

O. setosa Heron, 1977 : 73, figs 22a–h.

DESCRIPTION. *Female.* Mean body length of 4 specimens 0·5 mm (range 0·42 to 0·58 mm). Body figured (Figs 8a–c). Appendages of *O. setosa* similar to those described by Heron with only minor differences apparent (Figs 8d–n).

Male. Ratio of prosome and urosome lengths 1·5 : 1 (Figs 9a and b). Body length of 1 specimen 0·58 mm. Head 1·2 times longer than wide. Proportional lengths of urosome segments and caudal rami 12 : 47 : 3 : 3 : 3 : 18 : 14 (Fig. 9c). Genital lappets extending postero-laterally into acute points.

Mouthparts like those of female, except first antenna and maxilliped. First antenna 4-segmented (Fig. 9d). Maxilliped 3-segmented (Fig. 9e); second segment bearing 2 spines on internal surface and 3 groups of setules; terminal claw bearing a stout internal basal spine.

First and second natatory legs like those of female, but terminal spines of third and fourth exopodites longer than those of female, being respectively 1·5 times and twice the length of terminal segments. Two spines, representing the fifth leg, borne on tubercle not clearly delimited from body.

Fifth Copepodid (female). Ratio of prosome and urosome lengths 3 : 1 (Figs 9f and g). Body length of 1 specimen 0·51 mm. Head 1·2 times longer than wide. Urosome 4-segmented (Fig. 9h). Proportional lengths of urosome segments and caudal rami 12 : 40 : 8 : 24 : 16. Mouthparts similar to those of adult female except maxilliped, bearing a group of setules on internal surface of second segment (Fig. 9i). Natatory legs bearing terminal spines proportionally longer than those of adult female (Figs 9j and k, 10a and b). (10j and k, 11a and b).

MATERIAL EXAMINED. 4♀♀ (1 lost), 1♂, 1♀ juvenile from sample 9541.24, 3980–3960 m, 20° N 21° W. BM(NH) 1981.127–129.

REMARKS. This species was identified by the cluster of spinules on the second segment of the second antenna, the armature of the maxilliped and the relative dimensions of the urosome segments. The female differs from Heron's description in some minor details: the terminal spines of the third and fourth endopodites are longer in proportion to their terminal segments in the present material. The male and the fifth copepodid have not previously been described. Heron reported *O. setosa* from 2 stations in the antarctic zone of the southwest Pacific between 1000 and 2000 metres depth.

Oncaea rotunda Heron, 1977

O. rotunda Heron, 1977 : 77–79, figs 24o–q, 25a–m.

DESCRIPTION. *Female.* body length of 1 specimen 0·55 mm. Body (Figs 10c–e) and second antenna (Fig. 10f) figured.

MATERIAL EXAMINED. 1♀ from sample 9541.24. 3980–3960 m, 20° N 21° W. BM(NH) 1981.130.

REMARKS. This specimen was assigned to *O. rotunda* because of its distinctive second antenna, which has a very short terminal segment relative to the second segment and bears relatively short terminal spines and setae. Also the terminal segment of the fourth endopodite is reduced. Although somewhat smaller than the type material (mean length 0·74 mm), this specimen otherwise corresponds closely to Heron's description. Heron reported *O. rotunda* from 3 stations in the antarctic zone of the Pacific between 1000 and 2000 metres depth.

Oncaea brocha Heron, 1977

O. brocha Heron, 1977 : 60, figs 14f–n, 15a–n.

DESCRIPTION. *Female.* Body length of 2 specimens 0·81 and 0·83 mm. Urosome (Fig. 10g), second antenna (Fig. 10h), maxilliped (Fig. 10i) and second and third natatory legs (Figs 10j and k) figured.

MATERIAL EXAMINED. 2♀♀ from sample 9541.24, 3980–3960. 20° N 21° W. BM(NH) 1981.131.

REMARKS. The specimens were identified by the following combination of characters: the relative lengths of the segments of the first and second antennae, the armature of the maxilliped, of the natatory and of the fifth legs. The second antenna has an additional terminal spine not figured by Heron. This may have been lost from Heron's material or may represent geographical variation. Another minor difference observed was the length of the terminal spines of the second and third endopodites which are relatively longer in the present material. The refractive granules mentioned by Heron are absent from these specimens, but but these may have been artefacts or may represent the positions of cuticular pores. Heron reported *O. brocha* from 1 station in the antarctic zone of the southwest Pacific between 1000 and 2000 metres depth.

Oncaea schmitti (Heron, 1977) Comb. nov.

Epicalymma schmitti Heron, 1977 : 82–84, figs 28a–n, 29a–e.

DESCRIPTION. *Female.* Body length 2 specimens 0·33 and 0·34 mm. Body (Figs 11a and b), second antenna (Fig. 11c) and maxilliped (Fig. 11d) figured.

MATERIAL EXAMINED. 2♀♀ from sample 9541.24, 3980–3960 m. 20° N 21° W. BM(NH) 1981.132.

REMARKS. This species is here transferred from the genus *Epicalymma* to *Oncaea* (for discussion see page 191). Specimens are clearly identifiable as *O. schmitti* by the armature and relative segment lengths of the second antenna, the armature of the maxilliped and the dorsal projections of the caudal rami. However, the specimens are so thinly chitinized that the genital segment had partially collapsed during capture or preservation. Therefore, the drawing of the urosome may not represent the morphology of the living animal. This species has also been recorded from the antarctic zone of the southwest Pacific where it was taken between 1000 and 2000 metres depth.

Oncaea umbonata (Heron, 1977) Comb. nov.

Epicalymma umbonata Heron, 1977 : 84–86, figs 29f–p, 30a–c.

DESCRIPTION. *Female.* Body length of 1 damaged specimen 0·62 mm, without caudal rami. Body (Figs 11e and f), second antenna (Fig. 11g) maxilliped (Fig. 11h) figured.

MATERIAL EXAMINED. 1♀ from sample 9541.24, 3980–3960 m. 20° N 21° W. BM(NH) 1981.133.

REMARKS. This species is here transferred from the genus *Epicalymma* to *Oncaea* (for discussion see below). Although the specimen lacks its caudal rami it was assigned to *O. umbonata* on the basis of its body size and maxilliped armature. There are also differences of the armature of the second antenna between this and the specimens recorded as *O. schmitti*, the two species are otherwise very close. The natatory legs and other mouthparts correspond closely to Heron's original description. This species has also been recorded from the antarctic zone of the southwest Pacific where it was taken between 1000 and 2000 metres depth.

Phylogenetic relationships within the genus *Oncaea*

Giesbrecht (1892) designated the following character states as typical of the genus *Conaea*: the elongate terminal segment of the second antenna with very large, hook-tipped spines; endopodite of the fourth leg shorter than the exopodite, third segment is reduced (shorter than the first or second segment); the fifth leg reduced to a single plumose seta. However Heron (1977) was able to demonstrate the presence of a minute spinule accompanying the seta of the fifth leg of *O. gracilis* Dana, 1852 (= syn. *C. rapax*), the type species. Heron also described 2 new species of *Conaea, C. succurva* and *C. hispida.* Both of these have a seta on a small prominence representing leg 5, and a reduced endopodite of the fourth leg, but the third endopodite segment exceeds the first segment in length. These 2 species also lack the hooked tips to the terminal spines of the second antenna. *Oncaea expressa* Gordejeva, 1973 shares these and other character states but differs in the morphology of the natatory legs (Table 1). No less than 27 other species of *Oncaea* also show 1 or more of these *Conaea*-like character states (Table 2) The 2 species of *Epicalymma* which Heron (1977) described also exhibit the following character states: elongate terminal segment of the second antenna with very large hook-tipped spines, endopodite of the fourth leg shorter than the exopodite, third segment reduced (but *longer* than the first or second segment), fifth leg with a single terminal seta.

A continuous gradation of character states within *Oncaea, Conaea* and *Epicalymma* is thus becoming apparent as more species of *Oncaea* are discovered. The armature of the third exopodite segments of the swimming legs also illustrates this. Most *Oncaea* species have an external spine formula of III, III, II, II but there is considerable variation within the genus: II, III, III, I (*O. ancora* Gordejeva, 1973); III, III, III, II (*O. minor* Shmeleva, 1979 and *O. parobscura* Shmeleva, 1979); III, II, II, I (*O. expressa* Gordejeva. 1973); III, II, II, II (*O. brodskii* Shmeleva, 1968 and *O. longipes* Shmeleva, 1968); II, III, II, I (*O. exigua* Farran, 1908); II, II, I, I (*O. atlantica* Shmeleva, 1967 and *O. vodjanitskii* Shmeleva and Delalo, 1969; II, III, II, II (*O. zernovi* Shmeleva, 1966 and *O. mollicula* Gordejeva, 1975). The typical formula for *Conaea* is II, III, II, I and for *Epicalymma* II, III, III, I. Such variation represents a continuum which cannot, in my opinion, justifiably be subdivided into 2 or more genera as it is at present. It is probable that *Conaea*-like and *Epicalymma*-like character states have been derived by reduction and loss of armature elements from ancestors within the genus *Oncaea*. Separation of the *Conaea* and *Epicalymma* species would leave

Table 1 Comparison of morphology of natatory legs of *Oncaea expressa. O. succurva* and *O. hispida.*

	Leg 1	Leg 2	Leg 3	Leg 4
O. expressa Gordejeva, 1973	Exopod. spine 2 × length term. segm. Endopod. spine shorter than term. segm.	Exopod. spine 2 × length term. segm. Endopod. spine 1·5 × length term. segm.	Exopod. spine 2·5 × length term. segm. Endopod. spine >4 × length term. segm	Exopod. spine >2× length term. segm. Endopod. spine >4 × length term. segm.
O. succurva (Heron, 1977) comb. nov. (syn. *Conaea succurva*)	Exopod. spine 2 × length term. segm. Endopod. spine same length term. segm.	Exopod. spine >2 × length term. segm. Endopod. spine 1·5 × length term. segm.	Exopod. spine 2·5 × length term. segm. Endopod. spine 2·5 × length term. segm.	Exopod. spine >2·5 × length term. segm. Endopod. spine 3 × length term. segm.
O. hispida (Heron, 1977) comb. nov. (syn *Conaea hispida*)	Exopod. spine 2 × length term. segm. Endopod. spine same length term. segm.	Exopod. spine >2× length term. segm. Endopod. spine 1·5 × length term. segm.	Exopod. spine 2·5 × length term. segm. Endopod. spine 2 × length term. segm.	Exopod. spine >3 × length term. segm. Endopod. spine >4 × length term. segm.

Oncaea as a paraphyletic group. In order to retain *Oncaea* as a monophyletic group (*sensu* Hennig, 1966) it is proposed that *Conaea* and *Epicalymma* be synonymized with *Oncaea* and that the species of *Conaea* and *Epicalymma* be transferred to *Oncaea, C. gracilis, C. succurva,* and *C. hispida* becoming *O. gracilis, O. succurva* and *O. hispida*, also *E. schmitti* and *E. umbonata* becoming *O. schmitti* and *O. umbonata* respectively.

Kazatchenko and Andreev (1977) described *Myctospictosum* as a genus of uncertain taxonomic position. A single male of *M. philippinensis* was found on the gills of *Myctophum spinosum* in the western Pacific. It is clear from the figures (Kazatchenko and Andreev, 1977 : Figs 9 and 10) that this is an oncaeid. It has the body shape, the 4-segmented first antenna and the 3-segmented second antenna of a typical *Oncaea* male. The other mouthparts have been interpreted differently by the authors but are clearly those of a male *Oncaea.* The natatory legs are also typical of the genus. It is proposed, therefore, that *Myctospictosum* should be synonymized with *Oncaea.* The armature of the natatory legs and the relative lengths of the posterior segments separate *O. philippinensis* comb. nov. from any of the known males of the genus *Oncaea.*

Oncaeids are often found clinging by their maxillipeds to other organisms and debris in plankton samples, there is, therefore, no reason to suppose that *O. philippinensis* is parasitic, it is probably a free-living planktivore like other species of the genus.

The generic diagnosis of *Oncaea* is ammended as follows:

ONCAEA Philippi, 1843

Oncaea Philippi, 1843 : 63.
Antaria Dana, 1846 : 229.
Conaea Giesbrecht, 1891 : 477.
Epicalymma Heron, 1977 : 82.
Myctospictosum Kazatchenko and Andreev, 1977 : 47.

Diagnosis. Cyclopoid shape. Rostral area thickened with rounded posteroventral margin. Female urosome 5-segmented, male 6-segmented. First antenna 6-segmented in female,

Table 2 *Conaea*-like character states exhibited by species of *Oncaea*.

Terminal segment of second antenna elongate	Endopod. 4 shorter than expod.	Leg 5 reduced to 1 seta, borne/not borne on a tubercle	3 of terminal setae of second antenna hook-tipped	Terminal segment of endopod. 4 shorter than first and second segments	
+	+	+	+	+	*O. gracilis* (Dana, 1852)
+	+	+	+		*O. schmitti* (Heron, 1977)
+	+	+	+		*O. umbonata* (Heron, 1977)
+	+	+			*O. ancora* Gordejeva, 1973
+	+	+			*O. atlantica* Shmeleva, 1967
+	+	+			*O. exigua* Farran, 1908
+	+	+			*O. expressa* Gordjeva, 1973
+	+	+			*O. hispida* (Heron, 1977)
+	+	+			*O. mollicula* Gordejeva, 1975
+	+	+			*O. succurva* (Heron, 1977)
+		?			*O. alboranica* Shmeleva, 1979
+		+			*O. prendeli* Shmeleva, 1966
+		+			*O. shmelevi* Gordejeva, 1972
+		+			*O. tenella* Sars, 1916
+		+			*O. tregoubovi,* Shmeleva, 1968
+	+				*O. brodskii* Shmeleva, 1968
+	+				*O. heronae* sp. nov.
+	+				*O. longpipes* Shmeleva, 1968
+	+				*O. memorata* Gordejeva, 1973
+	+				*O. minima* Shmeleva, 1968
+	+				*O. rotunda* Heron, 1977
+	+				*O. rotundata* Boxshall, 1977
+					*O. subtilis* Giesbrecht, 1892
+	+				*O. vodjanitskii* Shmeleva & Délalo, 1969
+	+				*O. zernovi* Shmeleva, 1966
		+			*O. ornata* Giesbrecht, 1891
	+				*O. infantula* Gordejeva, 1972
+					*O. africana* Shmeleva, 1979
+					*O. curvata* Giesbrecht, 1902
+					*O. englishi* Heron, 1977
+					*O. ivlevi* Shmeleva, 1966

4-segmented in male, both with long third segment. Second antenna 3-segmented, terminal segment bearing proximal group of 3 or 4 setae and a distal group of 6 to 8 setae. Mandible bearing 2 blades and 2 or 3 setae. First maxilla bilobed, inner lobe with 3 elements. Second maxilla with setose claw. Maxilliped 4-segmented in female and 3-segmented in male, second segment in female bearing 2 setae on the internal surface. Terminal segment produced as a long, curved claw. Legs 1–4 3-segmented, endopodites slender. Exopodites armed with serrate spines on external margin. Leg 5 reduced to small rod or knob-like segment fused to urosome somite and bearing 1 or 2 apical setae. Gender feminine.

TYPE SPECIES: *Oncaea vensusta* Philippi, 1843. Sixty-eight species of *Oncaea* are now known, over half of which have been described within the past 15 years (Shmeleva, 1966, 1967, 1968, 1969, 1979; Razouls, 1969; Gordejeva, 1972, 1973, 1975; Boxshall, 1977; Heron, 1977; Kazatchenko and Andreev, 1977).

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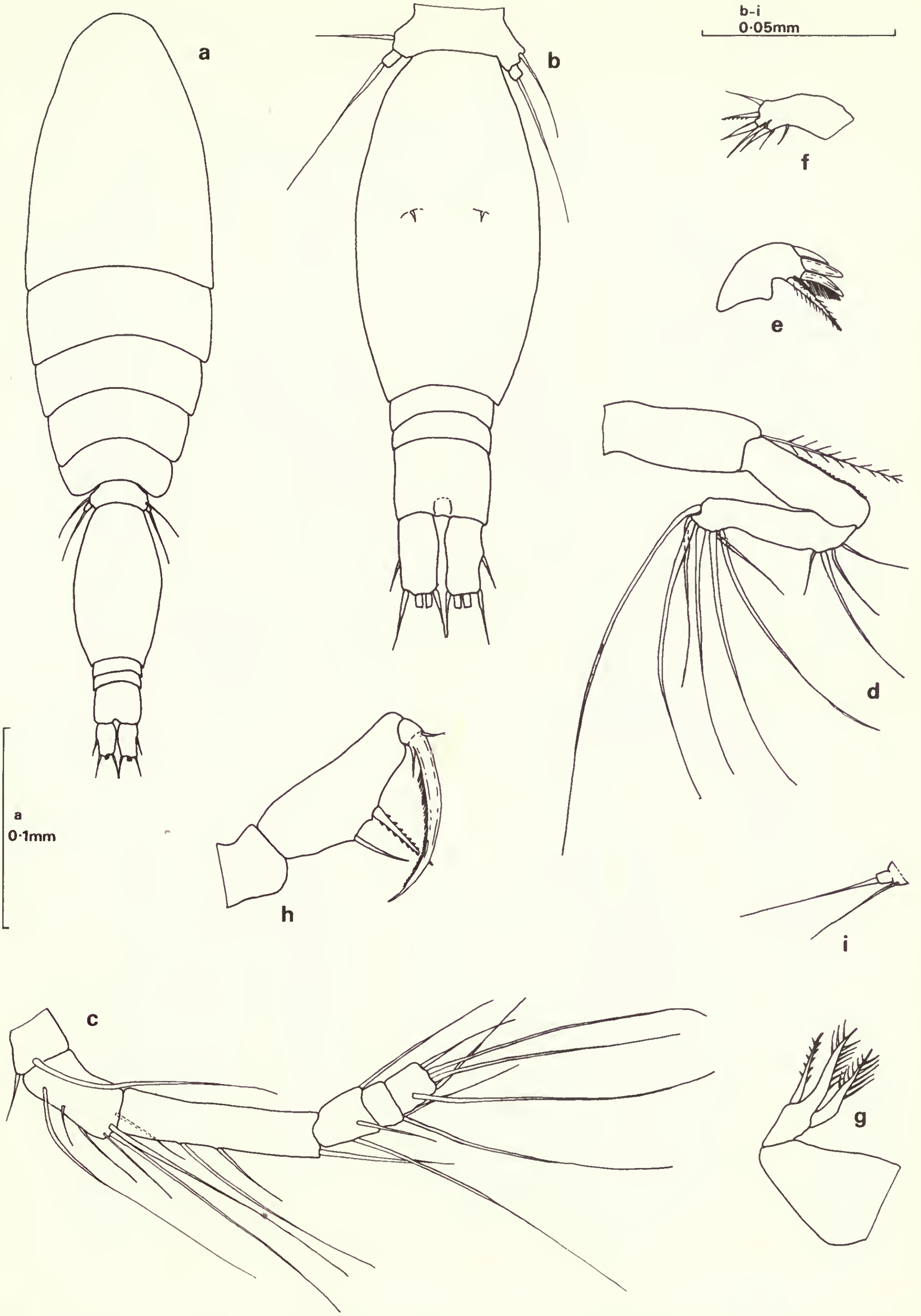
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Fig. 1 *Oncaea tregoubovi.* a. female, dorsal; b. urosome, dorsal; c. first antenna; d. second antenna; e. mandible; f. first maxilla; g. second maxilla; h. maxilliped; i. fifth leg.

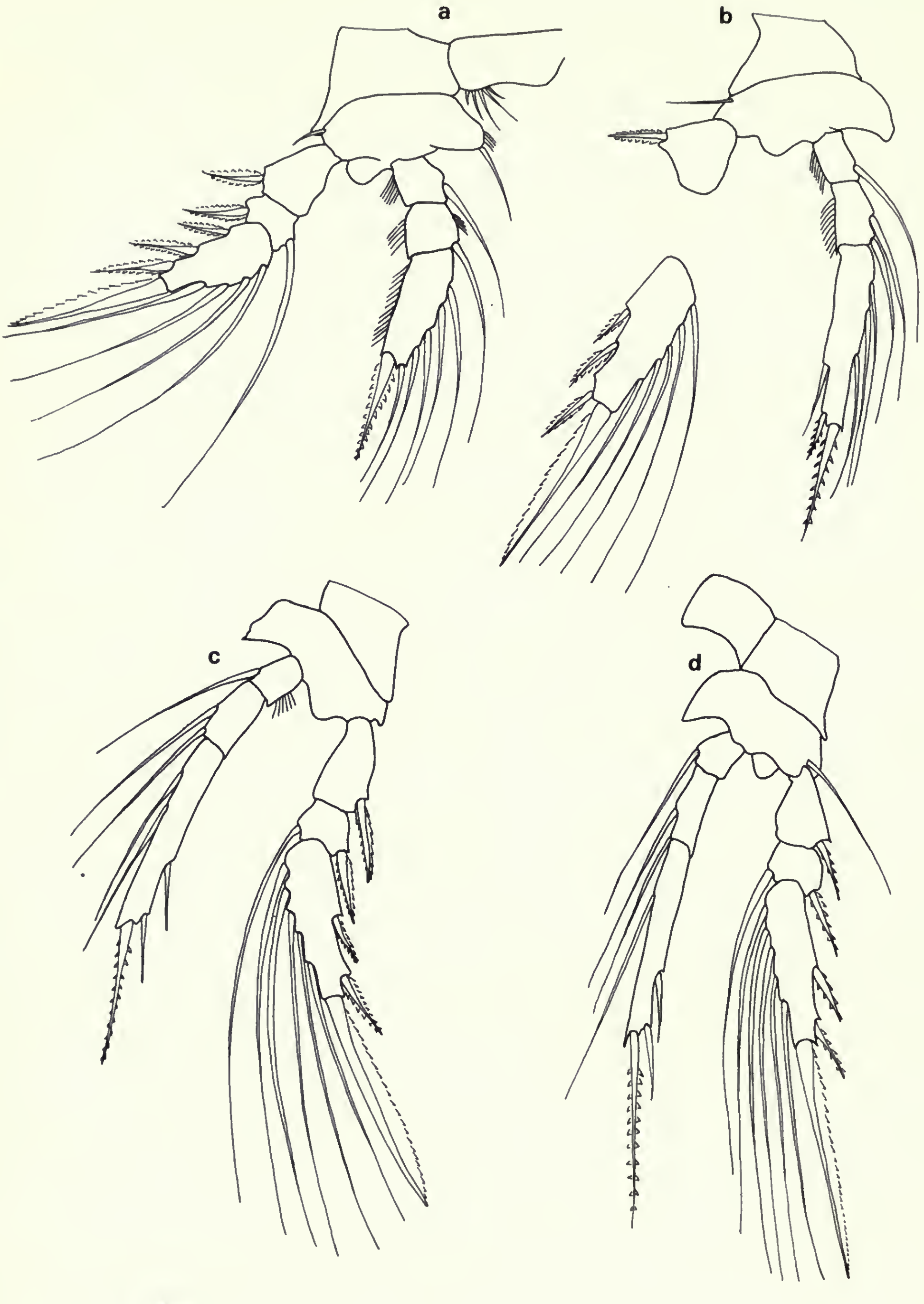
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Fig. 2 *Oncaea tregoubovi.* a. female, leg 1; b. leg 2 (damaged); c. leg 3; d. leg 4.

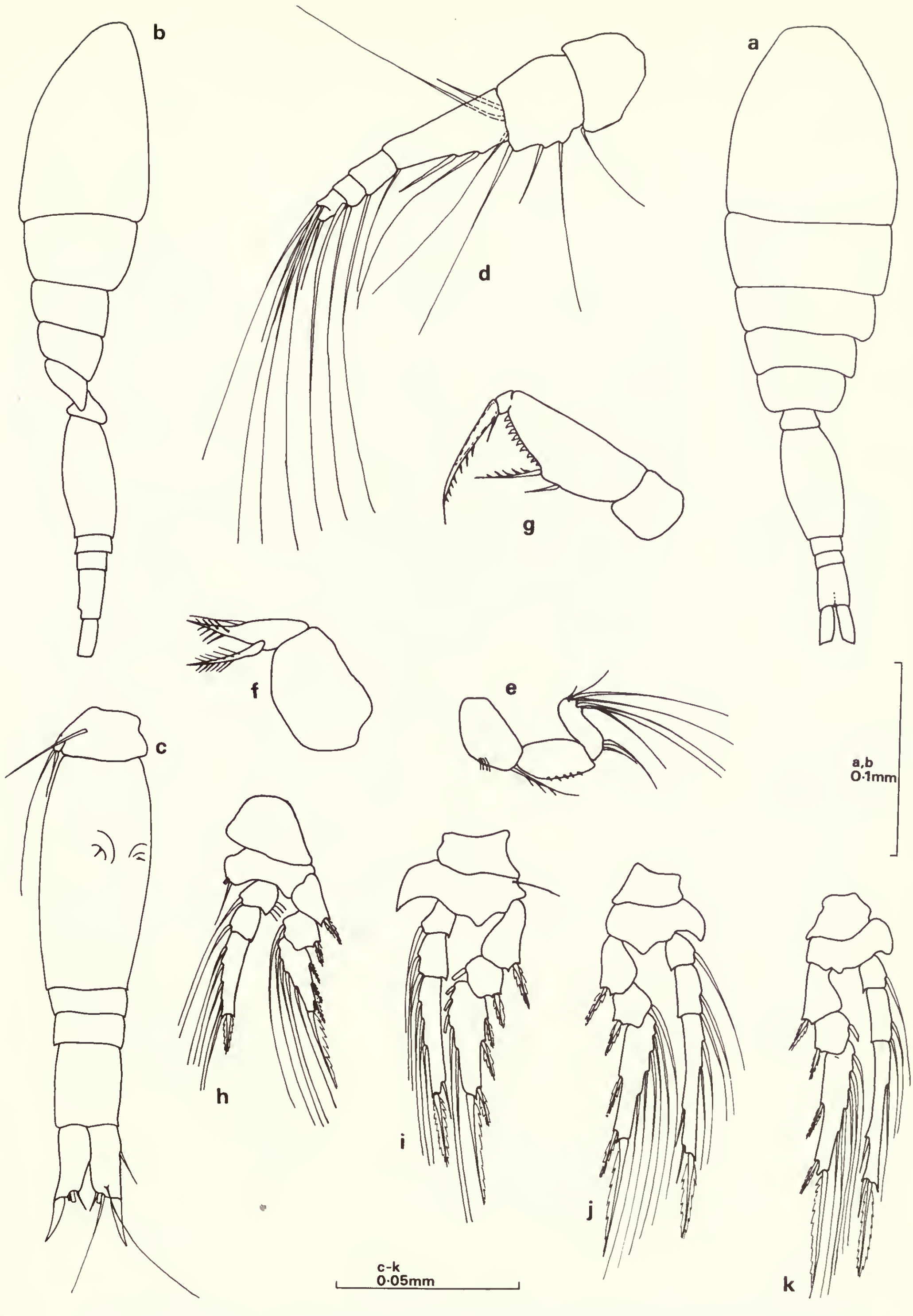
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Fig. 3 *Oncaea ivlevi*. a. female, dorsal; b. female, lateral; c. urosome, dorso-lateral; d. first antenna; e. second antenna; f. second maxilla; g. maxilliped; h. leg 1; i. leg 2; j. leg 3; k. leg 4.

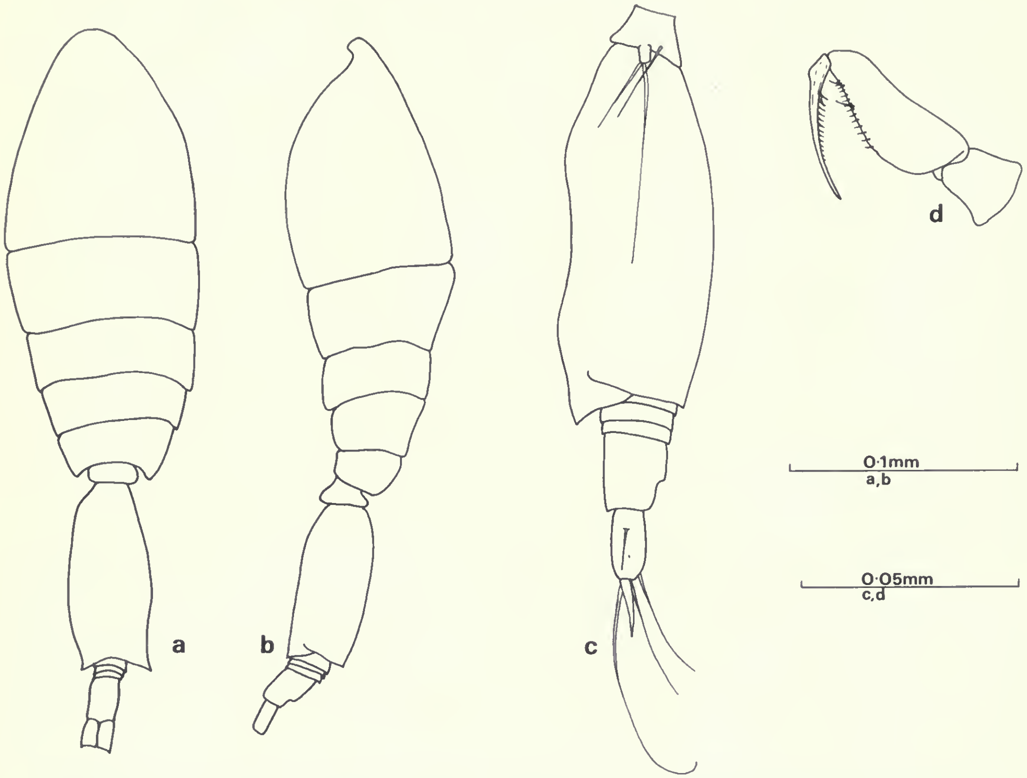
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Fig. 4 *Oncaea ivlevi.* a. male, dorsal; b. male, lateral; c. urosome, lateral; d. maxilliped.

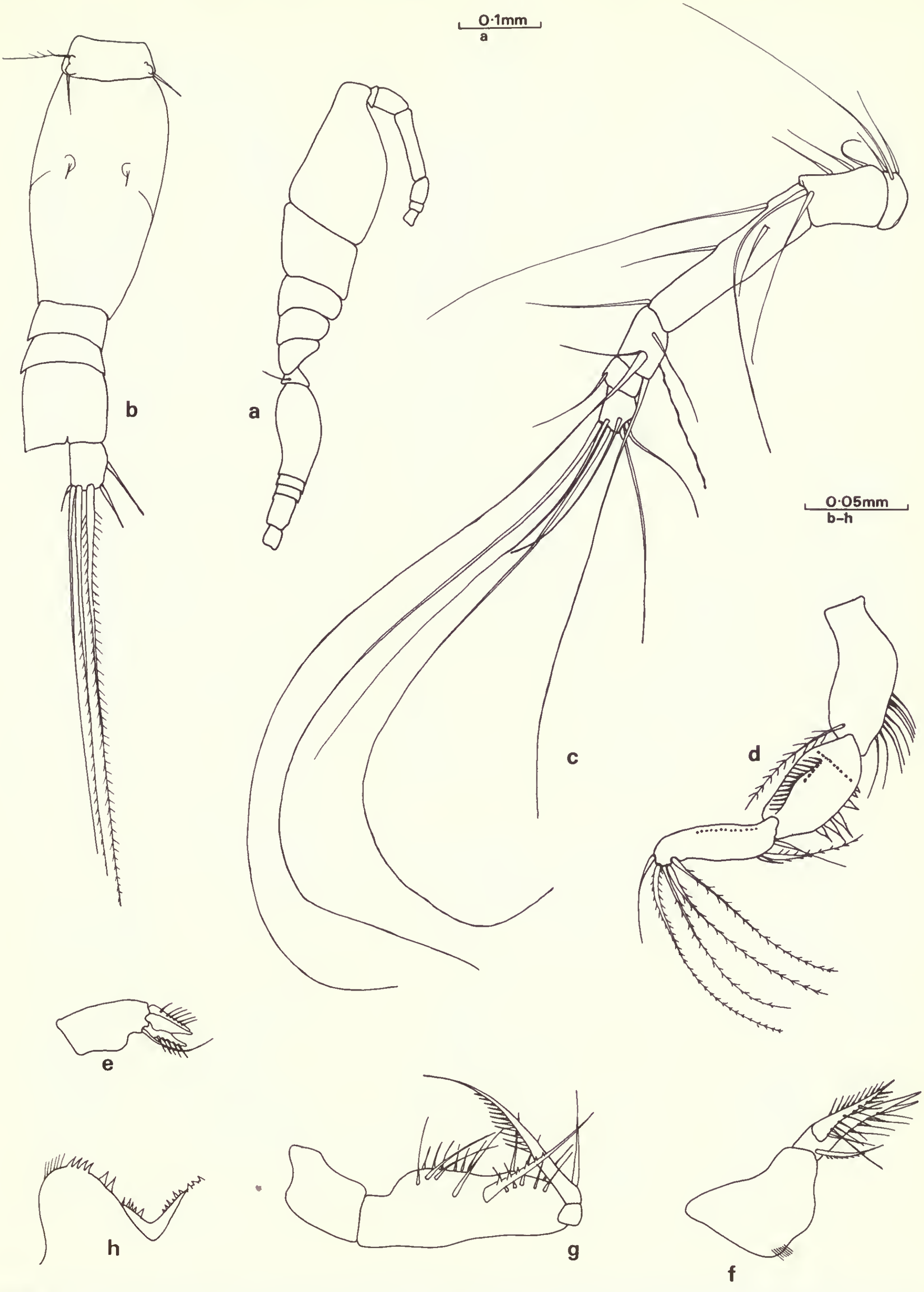
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Fig. 5 *Oncaea hispida*. a. female, lateral; b. urosome, dorsal; c. first antenna; d. second antenna; e. mandible; f. second maxilla; g. maxilliped; h. labrum (lamella missing).

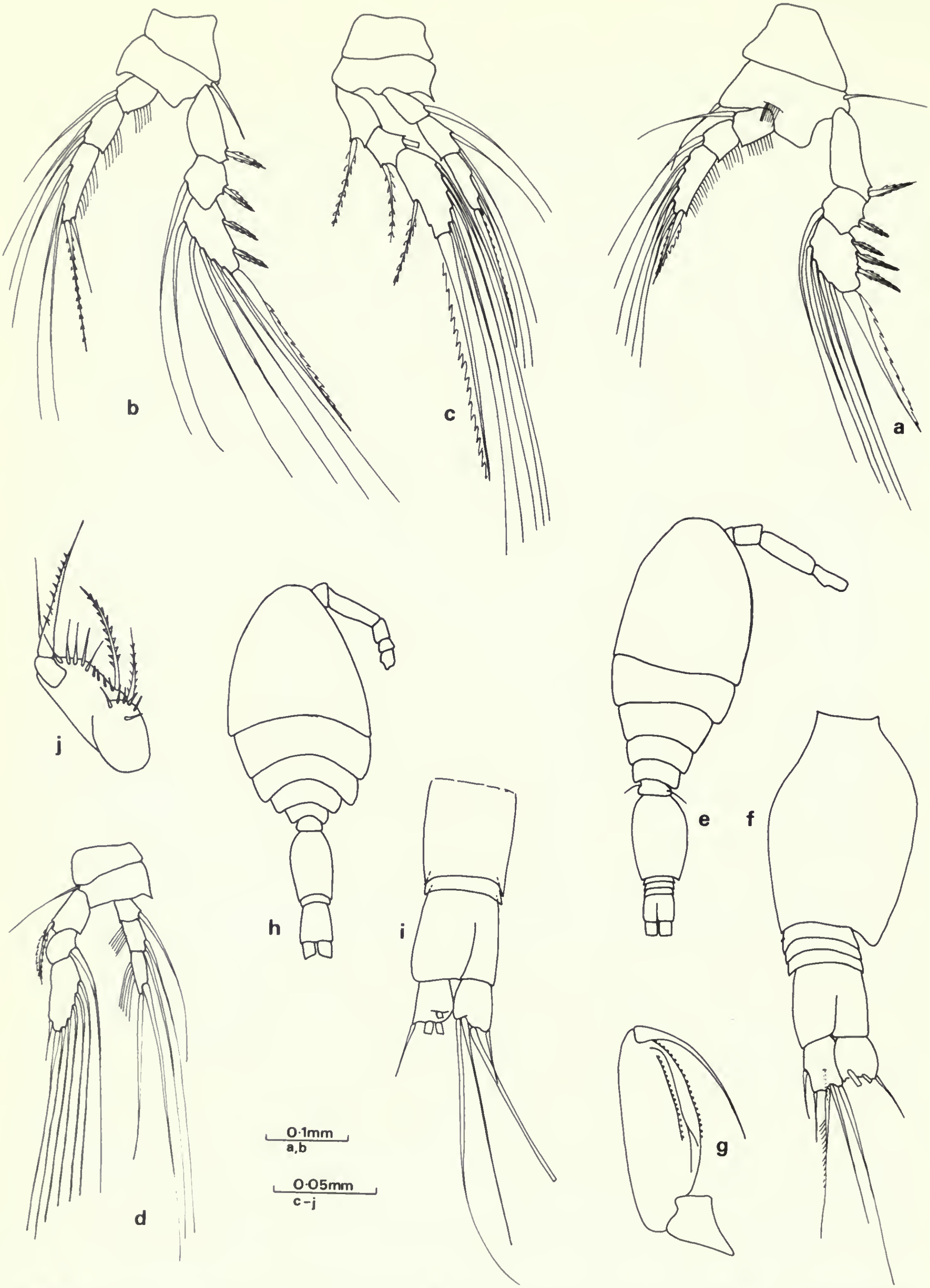

Fig. 6 *Oncaea hispida.* a. female, leg 1; b. leg 2; c. leg 3; d. leg 4; e. male dorsal; f. urosome ventral (specimen distorted); g. maxilliped; h. female copepodid V, dorsal; i. posterior segments of urosome, dorsal (only posterior half of genital segment figured); j. maxilliped.

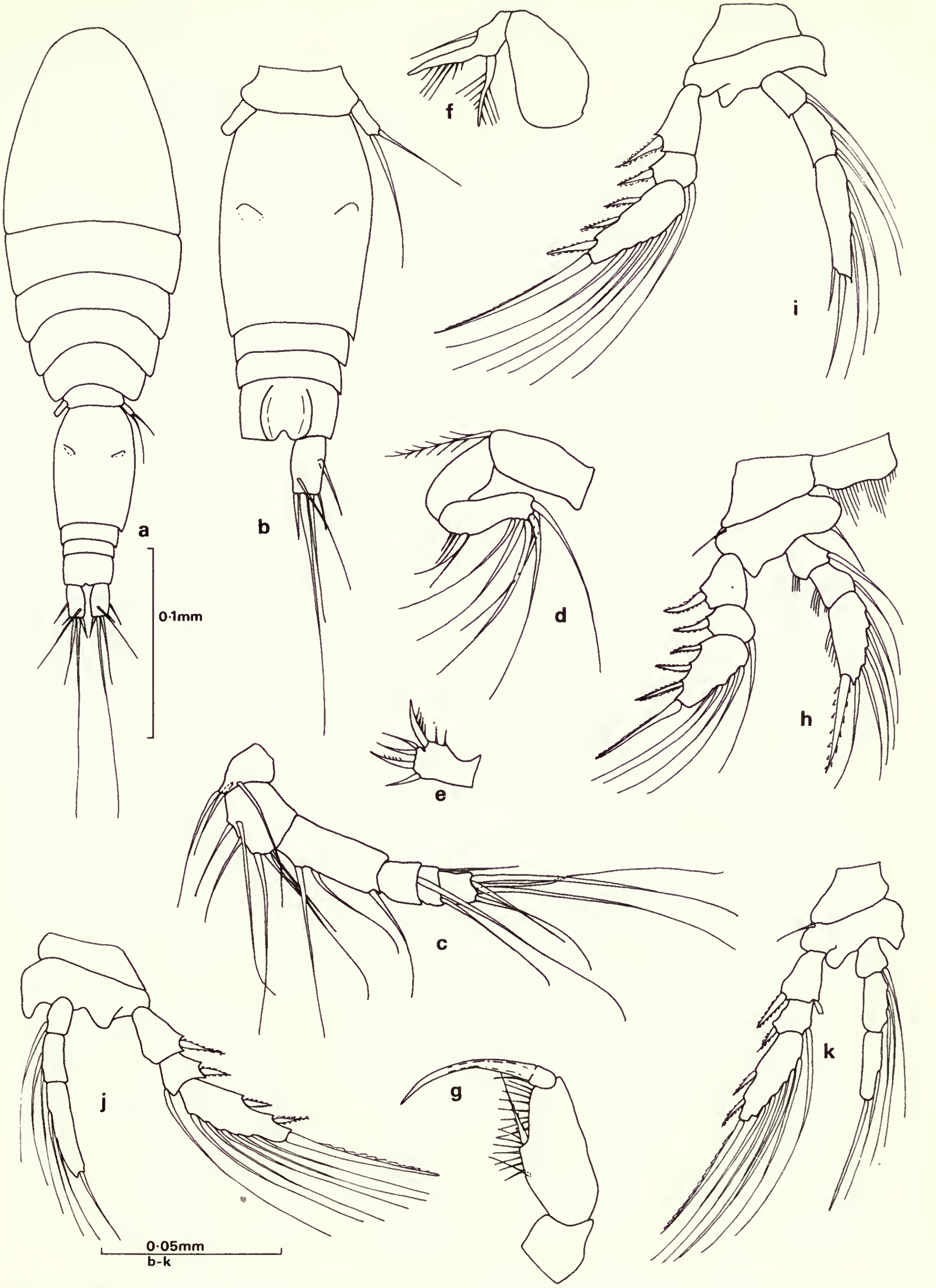
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Fig. 7. *Oncaea heronae* sp. nov. a. female, dorsal; b. urosome, dorsal; c. first antenna; d. second antenna; e. first maxilla, f. second maxilla; g. maxilliped; h. leg 1; i. leg 2; j. leg 3; k. leg 4.

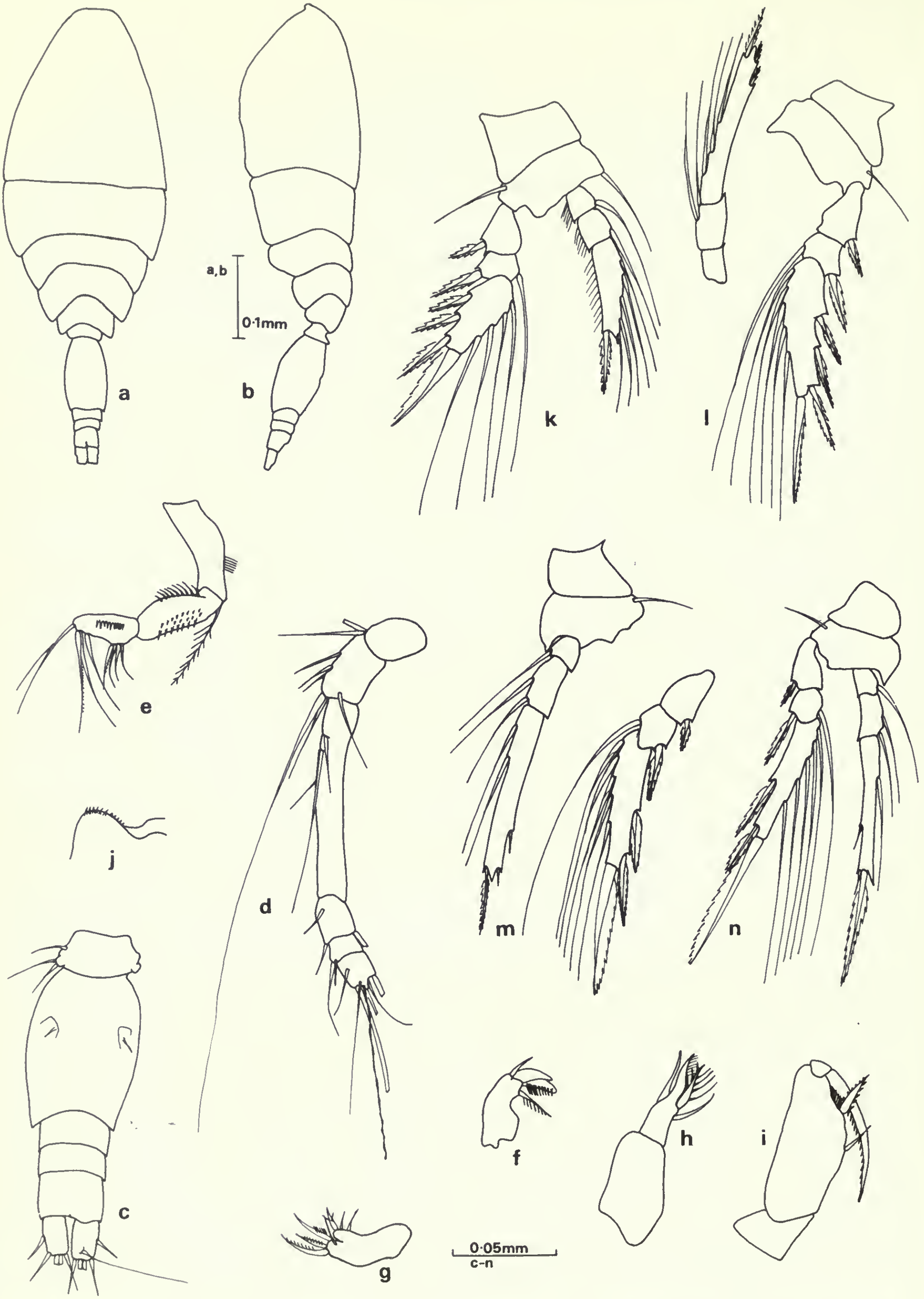
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Fig. 8 *Oncaea setosa.* a. female, dorsal; b. female, lateral; c. urosome, dorsal; d. first antenna; e. second antenna; f. mandible; g. first maxilla; h. second maxilla; i. maxilliped; j. labrum (lamella missing); k. leg 1; l. leg 2; m. leg 3; n. leg 4.

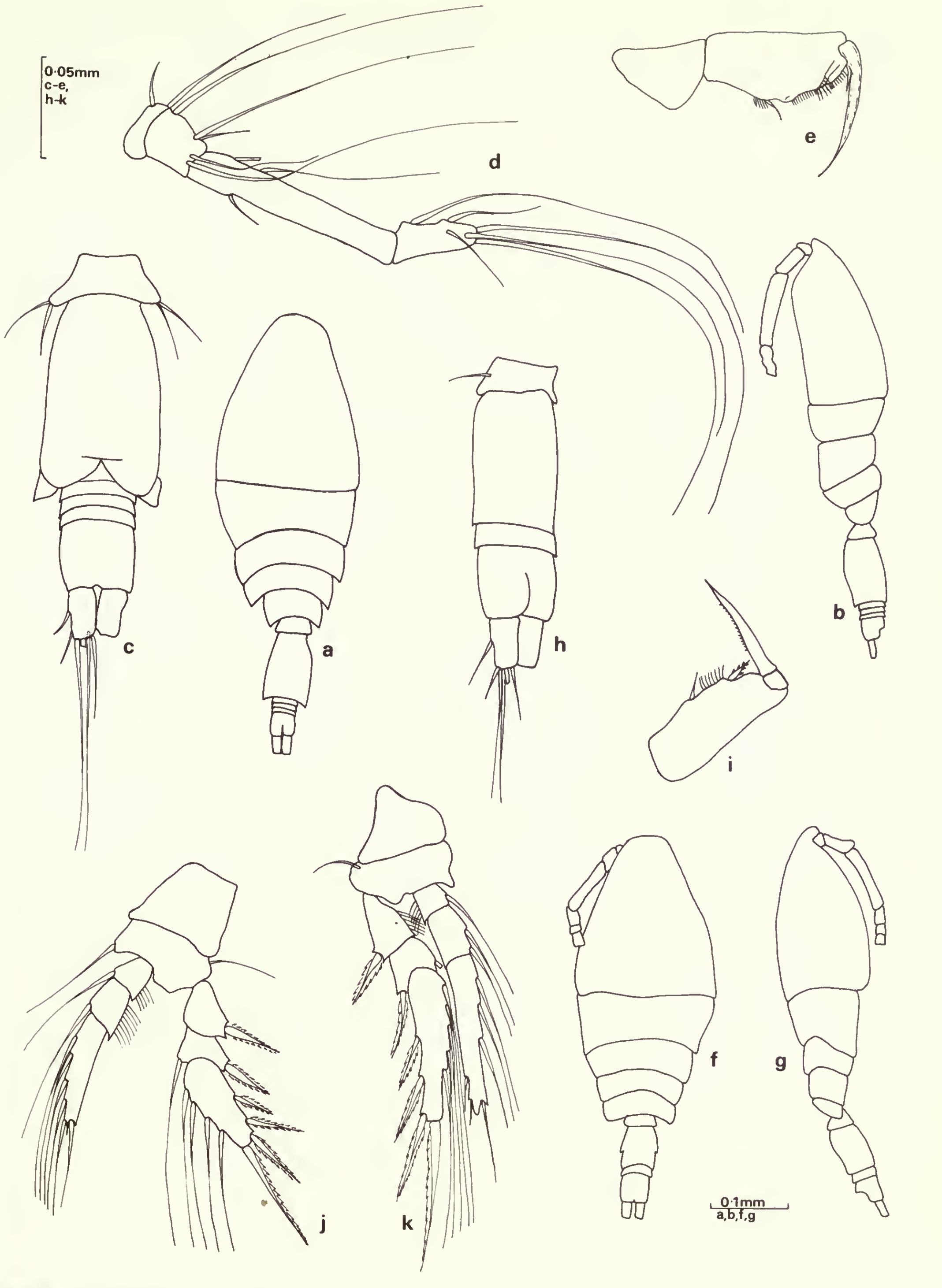
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Fig. 9 *Oncaea setosa.* a. male, dorsal; b. male lateral; c. urosome, ventral; d. first antenna; e. maxilliped (distal spine missing); f. female copepodid V, dorsal; g. female copepodid V, lateral; h. urosome, dorso-lateral; i. maxilliped; j. leg 1; k. leg 2.

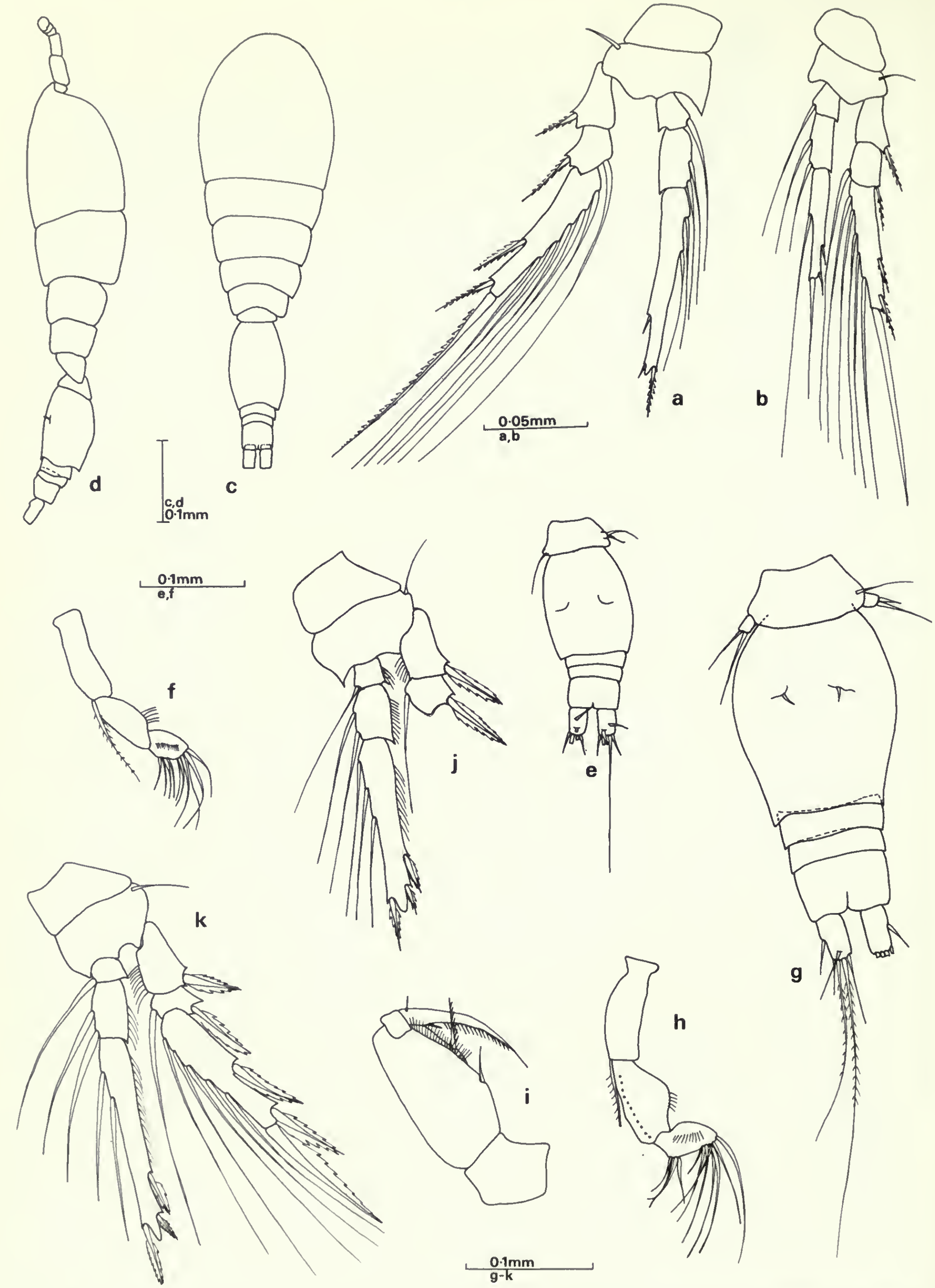
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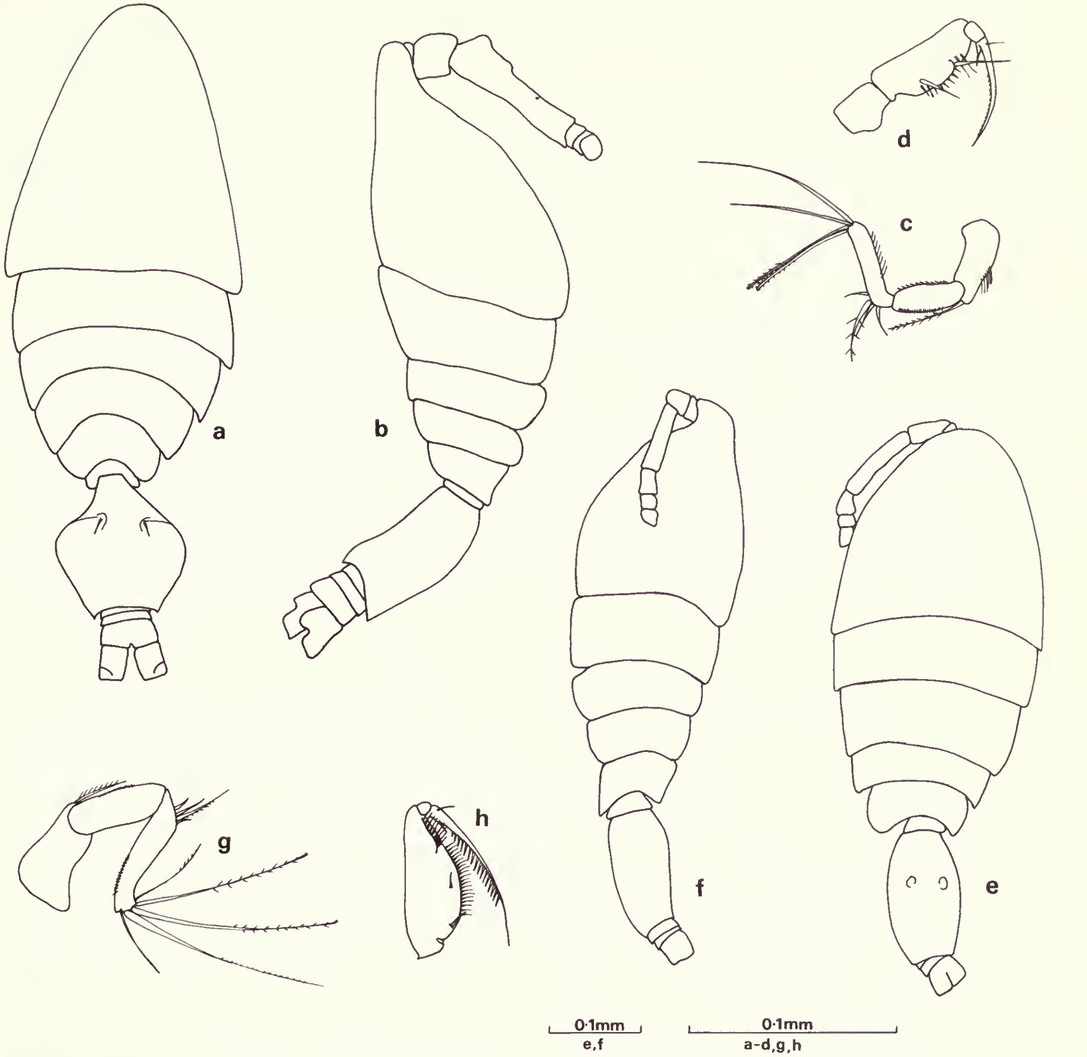
Fig 10 *Oncaea setosa.* a. female copepodid V, leg 3; b. leg 4; *Oncaea rotunda.* c. female, dorsal; d. female, lateral; e. urosome, dorsal; f. second antenna; *Oncaea brocha.* g. female urosome, dorsal; h. second antenna; i. maxilliped; j. leg 2; k. leg 3.


d
c
a
b
f
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g
h
0·1mm
e,f
0·1mm
a-d,g,h

Fig 11 *Oncaea schmitti.* a. female, dorsal; b. female, lateral; c. second antenna; d. maxilliped; *Oncaea umbonata.* e. female, dorsal; f. female, lateral; g. second antenna; h. maxilliped.

Larval and post-larval development of the Slender-legged Spider Crab, *Macropodia rostrata* (Linnaeus) (Oxyrhyncha : Majidae : Inachinae), reared in the laboratory

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Introduction

The Slender-legged Spider Crab *Macropodia rostrata* (Linnaeus) occurs northward to about latitude 65° N and southward to the Moroccan coast and Mediterranean (see Christiansen, 1969; Monod, 1932; Zariquiey Alvarez, 1968). West African and Cape Verde Island specimens have been assigned recently to *M. spinulosa* (Miers) (see Manning & Holthius, 1981). *M. rostrata* has been reported also from False Bay, S. Africa (see Barnard, 1950).

Previous descriptions (see p. 207) of larval stages of *M. rostrata* are not sufficiently detailed for comparative studies. In 1974 larvae of this species were reared from crabs collected from Tunisian and Plymouth waters and in 1977 from specimens obtained off the Isle of Man. These rearings provided material for the present detailed description and comparisons of the larvae and first crab stages of *M. rostrata* from three localities within its range of distribution.

Materials and methods

Ovigerous crabs were trawled from the following localities. (1) Off Port Erin, Isle of Man. 20–24 m., 24–25.3.1977. (2) S.W. of Eddystone Lighthouse, nr. Plymouth, Devon, 90 m., 18.6.1974. (3) Off Carthage-Salammbo, Tunisia, 4·5 m., 20.2.1974.

Larvae were reared using methods described by Rice & Ingle (1975 : 104) and Ingle & Clark (1977). Material was fixed in Steedman's fixative (Steedman, 1976 : 148) and later transferred to 70% alcohol. Drawings and measurements were made with the aid of a *camera lucida*. Measurements given are: (*a*) distance from base to tip of dorsal spine (D.S.); (*b*) carapace length, from between eyes to posterio-lateral carapace margin (C.L.).

All material has been incorporated into the Collections of the British Museum (Natural History), accession no;– 1981 : 201–225. Drawings and descriptions (unless otherwise indicated) are of specimens from locality (1). Ten specimens of each stage were dissected and examined from each locality except for ZII of Tunisian material of which 20 specimens were dissected to confirm the absence of a seta on the outer margin of the maxillule basis (see p. 210).

Whilst in the rearing laboratory females and larvae were maintained at 15°C. Larvae from locality (1) hatched within 10–12 days and those from (2) within 6–7 days of collecting the females. Both hatchings took an average of 30 days to reach first crab stage. Those from locality (3) hatched within 14 and 63 days respectively from time of collecting and an average of 22 days elapsed before the appearance of first crab stage.

Descriptions

Larval references. *Macropodia phalangium*:– Thompson, 1836 : 371, fig. e (pre-1st zoea), non fig. 2 = ?

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Hyas sp. ? *Stenorhynchus rostrata*:– Stuxberg. 1874 : 3 (1st zoea). ? *Stenorhynchus phalangium*:– Cano, 1893 : Tav. 35, figs 70, 72, 74, 77–85 (1st zoea, megal. crab). *Macropodia rostrata*:– Lebour, 1928 : 550, Pl. III, fig. 10 (coloured), Pl. XV, fig 7, Pl. XVI, figs 3, 5, 8 (prezoea, 1st, 2nd zoeae, megal. 1st crab), non *Stenorhynchus phalangium*:– Lo Bianco, 1904 : 439; 1904 : Taf. 12, fig 43 (= ? *Inachus* megalopa).

FIRST ZOEA

Dimensions: D.S. 1·3–1·4 mm., C.L. 0·7–0·8 mm.

Carapace (Fig. 1a). Dorsal spine long and straight, narrowing distally. Rostral and lateral spines not developed. Dorso-median elevation conspicuous above which there is a small seta on either side; ocular eaves developed; a pair of small dorso-lateral setae near base of dorsal spine; posterio-lateral margin of carapace with 'majid' spine and 1–2 additional long thin setae (see inset Fig. 1a). Surface of carapace with minute spinules.

Eyes: Partly fused to carapace.

Antennule: (Fig. 2a). Unsegmented and with 2 terminal aesthetascs and 2 setae.

Antenna: (Fig. 2a). Spinous process without distal spinules: exopod slightly shorter than spinous process and with one small spinule in proximal half; endopod developed as acute bud.

Mandible: (Fig. 2b). Incisor and molar process developed, palp absent.

Maxillule: (Fig. 3a). Endopod 2-segmented (incipiently in some specimens), distal segment long and thin with 3 long distal setae; basal endite with 5 spines and 2 setae, coxal endite with 7 setae/spines.

Maxilla: (Fig. 4a). Endopod narrow, distally truncate and with 4 long setae; basal endite broad, distal margin concave or incipiently bilobed and with 4 + 5 setae; coxal endite incipiently bilobed, outer lobe with acute outer margin, with 3 + 4 setae respectively; scaphognathite with 10 long plumose marginal setae, posterior seta very stout.

First maxilliped: (Fig. 5a). Basis with 9 setae arranged 2, 2, 2, 3; endopod 5-segmented with 3, 2, 1, 2, 4 + 1 setae; exopod with 4 terminal natatory setae.

Second maxilliped: (Fig. 5b). Basis with one proximal seta; endopod 3-segmented with 0, 0, 3–4 + 1 setae; exopod incipiently (in some specimens) segmented with 4 terminal natatory setae.

Third maxilliped and pereiopods: Represented as incipient buds.

Abdomen: (Figs 6a, b, e). 5-segmented + telson; 2nd segment with a pair of anterio-laterally directed acute dorso-lateral processes; posterio-lateral processes on segments 3–5 long and terminally acute; a pair of minute setae near posterio-dorsal margins of segments 2–5. Telson furcae long and distally with minute spinules, each furca with a small lateral spine; inner medio-lateral margin of telson with 3 long plumed setae, innermost (in some specimens) noticeably short (see Fig. 6e); incipient pleopod buds on segments 2–5.

SECOND ZOEA

Dimensions: D.S. 1·1–1·2 mm., C.L. 0·8–0·9 mm.

Carapace (Figs 1b, c). Dorsal spine curved. Dorso-median elevation well developed; ocular eaves conspicuously expanded (Fig. 1c).

Eyes: Moveable.

Antennule: (Fig. 2c). With 6 aesthetascs and 1–2 setae.

Antenna: (Fig. 2c). Exopod with 2 proximal spinules; endopod slightly more than ⅓ length of exopod.

Mandible: (Fig. 2d). Each half dissimilar.

Maxillule: (Fig. 3b). Outer margin of basal endite with a seta, distal margin with 5 spines and 3 setae; coxal endite with 7 setae/spines.

Maxilla: (Fig. 4b). Endopod setation unchanged; basal endite with 5 + 5 setae; coxal setation unchanged; scaphognathite with 16 setae.

First maxilliped: (Fig. 5c). Setation on basis and endopod unchanged; exopod with 6 terminal natatory setae.

Second maxilliped: (Fig. 5d). Basis without setae; endopod with 0, 0, 3 + 1 setae; exopod with 6 terminal natatory setae.
Third maxilliped and pereiopods: Represented as conspicuous incipient buds.
Abdomen: (Fig. 6c, d). Posterio-lateral processes on segments 3–5 longer than in first stage; pleopod buds long.

MEGALOPA

Dimensions: C.L. 1·2–1·3 mm.
Carapace: (Figs 1d, e). Longer than broad, with a small obtuse rostrum and obtuse but prominent submedian lobes; frontal region with 2–3 median broad longitudinal tubercles, hepatic regions swollen, each protogastric region with a long anteriorly directed process narrowing distally; cardiac region with a posterio-dorsally directed spine.
Eyes: Large, with well developed cornea.
Antennule: (Fig. 2e). Peduncle 3-segmented, terminal segment with a seta on inner margin; exopod 2-segmented, proximal with 2 and distal segment with 4 aesthetascs.
Antenna: (Fig. 2f). Peduncle 3 segmented, proximal segment with a stout ventrally directed process, distal segment with a small ventral seta; flagellum 4-segmented, 2nd segment longest and with 4 setae, 4th segment with 2–3 aesthetascs.
Mandible: (Fig. 2g). Molar process slightly reduced, incisor prominent and broad; palp stout and unsegmented, with a small terminal seta.
Maxillule: (Fig. 3c). Endopod reduced; distal margin of basal endite with 6–7 spines and 6–7 setae, coxa with 6–7 setae/spines.
Maxilla: (Fig. 4c). Endopod reduced and terminally acute, with one long distal seta; basal endite broadly oval, with 6 + 3–4 setae, coxal endite with 3 + 3 setae; scaphognathite with 18–19 setae.
First maxilliped: (Fig. 7a). Coxa with 4, basis with 9–10 setae; exopod 2-segmented, distal segment with 4 setae; endopod reduced and terminally acute; epipod small.
Second maxilliped: (Fig. 7b). Exopod 2-segmented, proximal segment long, distal with 4 setae; endopod 4-segmented, 2nd (carpus) with one, 3rd (propodus) with 3 setae and 4th (dactylus) with one seta and 3 spines; epipod small (not shown in figure).
Third maxilliped: (Fig. 8a). Endopod 5-segmented, inner margin of ischium with few minute spinules and 7–9 short setae, merus with 4 setae, carpus with 3, propodus with 6 and dactylus with 4 setae; distal segment of exopod with 4 setae, epipod moderately well developed.
Pereiopods: (Figs 8c, 9a, 10a–c). Chelipeds moderately stout and sparsely setose, distal parts of propodus and dactylus curved; merus with small obtuse spinule on inner proximal margin; basis/coxa with small obtuse process on lower margin. Pereiopods 2–5 slender, setose and minutely spinulate, dactylus terminally acute, ischium of 2nd-3rd pereiopods with a prominent curved hook-shaped process.
Abdomen: (Figs 1f, g). 5-segmented + telson; 1st with 4, 2nd-3rd with 2 posterio-dorsal setae, 4th with 4 setae, 5th with 6 setae; telson broader than long, posterior margin subtruncate. A pair of well developed pleopods on segments 2–5, 4th pair smallest, exopod of each with 8 long plumose setae; endopod of each with 2 coupling hooks.

FIRST CRAB

Dimensions: C.L. 1·4–1·5 mm.
Carapace: (Fig. 1j). Slightly less that $1\frac{1}{2}\times$ longer than broad; frontal region slightly produced, submedian lobes obtuse and with clusters of hook-setae, each protogastric region with a tubercle; orbits long, hepatic regions swollen, epibranchial regions slightly expanded, mesogastric with 2 median cristate tubercles, cardiac region with a prominant tubercle, intestinal with a small median tubercle; dorsal surface and lateral margins of carapace with many hook-setae.
Eyes: Large and with a few hook-setae.
Antennule: (Fig. 2h). First and 3rd segments of peduncle with a seta; exopod indistinctly segmented, with 7–8 aesthetascs and 2–3 setae; endopod 2-segmented, with 2 terminal and 2 sub-terminal setae.

Antenna: (Fig. 2h). Peduncular segments with 2, 1–2, and 5 setae respectively; flagellum usually with 3 or 4 demarcated segments, with 3 subterminal setae as shown.
Mandible: (Fig. 2i). Molar process acute, incisor expanded as a broad cristate lobe; mandibular palp 2-segmented, distal segment with 2 setae.
Maxillule: (Fig. 3d). Endopod very reduced, outer margin of basal endite with a prominent seta, margin with 8 spines and 4 setae; coxal endite with 9 setae/spines.
Maxilla: (Fig. 4d). Endopod very reduced and with one apical seta; basal endite with 10 and coxal with 2–3 setae respectively; scaphognathite with 20–21 short plumose setae.
First maxilliped: (Fig. 7c). Coxa with 10–11 setae, basis with 10 setae; distal segment of exopod with 3 long setae; endopod sub-triangular, with 1–2 small setae on distal margin; epipod well developed and with 6 setae.
Second maxilliped: (Fig. 7d). Merus with 2 setae, propodus with 4 setae and a distal spine, dactylus with 1–2 setae and 4 spines; epipod small.
Third maxilliped: (Fig. 8b). Ischium with numerous setae (18–20) as shown, inner margin with 3–4 processes; merus with 3 setae, inner margin with an acute process; carpus, propodus and dactylus with 2, 4 and 5 setae respectively on outer surface and margins; distal segment of exopod with 3 short plumose setae; a cluster of short setae near coxal/epipod junction; epipod well developed.
Pereiopods: (Figs 8d, 9b, c, 10d, e). Cheliped moderately setose as shown; inner distal propodal margin with 3 acute to sub-acute teeth (see inset to Fig. 8d); distal part of the propodus acute and curved. Pereiopods 2–5 long, thin and with numerous setae; 2nd and 3rd similar in shape, 3rd longest (Fig. 9c); 4th and 5th similar in shape, dactylus curved, inner margin of dactylus of 4th (Fig. 10d) with 4 spines, of 5th with 2–3 spines.

Remarks

Comparisons of larvae and first crab stages of Mediterranean and British material of *M. rostrata* (see p. 207) have revealed only two apparent morphological differences. (1) all zoeae II examined from the Tunisian locality are without a seta on the outer margin of the maxillule basal endite; this seta is present in all zoeae II reared from the Plymouth and Isle of Man crabs. The presence of this seta is considered an important larval brachyuran feature (see Rice, 1980 : 299 as 'exopod' seta), and its absence in the Tunisian specimens cannot be explained. Clark (1980) also reported its absence from the maxillule of zoeae II *Inachus dorsettensis* (Pennant) reared from Isle of Man crabs but found it present in Plymouth material. (2) in the first crab stage of Tunisian specimens the carapace submedian lobes are widely spaced and the outline of the hepatic region is noticeably convex. By comparison, first crab stages from the two British localities are slightly smaller than the Tunisian specimens, the submedian lobes are closer together and the hepatic region outline is relatively straight (Fig. 1, cf j & k). These slight morphological differences observed in the first crab stages may express the extremes of geographical variation of *M. rostrata* since the Mediterranean material probably represents the near southernmost limit of this species (see p. 207). Ingle & Manning (in press) have drawn attention to the noticeable variation of carapace shape among population of pre- and post pubertal crabs of *M. rostrata* from the N.E. Atlantic and Mediterranean regions.

Four species of *Macropodia* are reported from N.E. Atlantic waters: *M. rostrata* (Linnaeus), *M. deflexa* Forest, *M. tenuirostris* (Leach) and *M. linaresi* Forest & Zariquiey Alvarez. Larval stages of the first three species mentioned were described briefly by Lebour (1927, 1928); larvae of *M. linaresi* are unknown.

Lebour (1927, 1928) recognized that the zoeae of *M. rostrata* and *M. deflexa* (= *egyptia*) has a longer and more straight dorsal spine, and longer antennae than *M. tenuirostris* (= *longirostris*); she also noted that the antennae of *M. deflexa* are longer than *M. rostrata*. Lebour remarked that the megalope of *M. rostrata* has shorter legs and a less deflected rostrum than *M. tenuirostris*, and that the 'central lobe' of the rostrum of *M. deflexa* protrudes more than that of *M. rostrata* but that otherwise the megalop of both species are 'hardly to be distinguished'.

Larval material of *M. deflexa* has not been available for examination during this study but it has been possible to compare the larvae of *M. rostrata* with those of *M. tenuirostris* reared from females collected off the Isle of Man during March 1977. These comparisons are listed in Table 1.

Table 1

Character	*M. rostrata*	*M. tenuirostris*
Zoea I		
Carapace length:	0·7–0·8 mm	0·9–1·0 mm
Dorsal spine length:	1·3–1·4 mm	1·0–1·1 mm
shape:	relatively straight	noticeably curved
Antenna, total length:	1·2–1·2 mm	0·9–1·0 mm
Second mxpd endop. 3rd sgmt:	4 + 1 setae	3 + 1 setae
Zoea II		
Carapace length:	0·8–0·9 mm	1·1–1·2 mm
Antenna, total length:	1·3–1·4 mm (exceeding C.L.)	1·1–1·2 mm (not exceeding C.L.)
Carapace dorso-median elevation:	pronounced	not pronounced
Maxilla, coxal endite:	average of 7 setae	average of 8 setae
scaphognathite:	average of 16 setae	average of 17 setae
Abdomen posterio-lateral spines:	long	longer than *rostrata*
Second mxpd endop. 3rd sgmt:	3–4 + 1 setae	3 + 1 setae
Megalopa		
Carapace length:	average 1·2 mm	average 1·5 mm
Carapace frontal region:	2–3 median longit. tubercles	continuous median carina
Carapace protogastric processes:	forming moderately wide U-shape	forming wide U-shape
Cheliped merus:	with a small spine but without secondary posterior spinule	with large spine and secondary posterior spinule

Lebour (1928) provided a key to the larvae of five oxyrhynch genera that occur in British waters; Bourdillon-Casanova (1960) extended this number to seven genera in her key to Mediterranean brachyuran larvae. From a study of reared material and of published accounts (see footnote to Table 2), it has been possible to tabulate a sufficient number of comparative larval features from which a provisional key has been constructed to facilitate the identification of larvae of all those oxyrhynch genera represented in the North East Atlantic Ocean north of about 48° 30′ N.

Detailed studies of larval stages of *Achaeus cranchii, Pisa tetraodon, Maja squinado, Macropodia linaresi* and *M. deflexa* are still required whilst the positive identity (see Rice, 1980 : 308) of the plankton caught zoea II attributed to *Dorynchus thomsoni* still remains to be established.

Table 2

Character **zoea**	*Hyas*[1]	*Rochinia*	*Maja*[2]	*Inachus*	*Macropodia*[4]	*Achaeus*[5]	*Eurynome*[6]	*Pisa*[7]	?*Dorynchus*[15]
Lateral spines on carapace + or –:	+	+	+	–	–	–	–	–	+
Carapace dorsal spine/carapace length:	longer	as long as	longer (ZI) shorter (ZII)	slightly longer	longer (ZI) slightly shorter (ZII *tenuirostris*)	as long as	as long as	shorter	shorter than
Carapace rostral spine + or – & size:	+ very long	+ long	+ long	–	–	–	+ long	+ very short	+ long
Telson median cleft + or –:	+	–	+	+	+	+	+	–[8]	+
Telson lateral spines + or – & size:	+ long	+ long	+ 2 present (1 long)	+ long	+ short	+ very long	+ long + 1 setule	+ small	+ very long
Telson medio-lateral spines lengths:	middle longest	about equal	middle longest	about equal	middle longest	middle longest	middle longest	about equal[9] (ZI); outermost longest (ZII)	outermost longest
Abdomen posterio-lateral spines:	long	long	short	long	long	long	obtuse (ZI) short (ZII)	short	long
2 setae on 1st abdominal segment:	+	+	–[3]	+ *leptochirus* – *dorsettensis* & *phalangium*	–	+	3 (ZII)	+[10]	+
Setae on 2nd abdominal segment:	1 pr (ZI) 2 prs (ZII)	1 pr (ZI) 2 prs (ZII)	1 pr	1 pr	1 pr	1 pr	1 pr	1 pr (ZI) 2 prs (ZII)	1 pair
Dorso-lateral proc. on 3rd abd. sgmt:	+	–	+	–	–	–	–	–	+ 4th–5th
Setal formula basis 1st maxilliped:	2,2,3,3	2,2,3,3,	2,2,3,3	2,2,3,3	2,2,2,3	.	2,2,3,3	2,2,3,3[11]	.
No. setae basis of 2nd maxilliped:	4	3	3	1 *leptochirus* 0 *dorsettensis* & *phalangium*	1 (ZI) 0 (ZII)	.	3	3[12]	1
Setal formula endopod 2nd maxilliped:	1,1,4 + 1	0,1,4 + 1	1,1,4 + 1	0,1,3 + 1	0,0,4 + 1 (*rostrata*: 0,0,3 + 1 (*tenuirostris*)	.	1,1,4 + 1	1,2,2 + 1[13]	0,3 + 1
Setal formula endopod maxillule:	1 + 6	1 + 6	1 + 6	0 + 4	0 + 3	.	1 + 6	1 +6[14]	0 + 5
Telson dorsal spine + or –:	+	–	+	–	–	–	+	–	–
megalopa									
No. abdominal segments (incl. telson):	7	7	7	6	6	6	7	7	.
No. pairs of pleopods (incl. uropods):	5	5	5	4	4	4	5	5	.
No. setae on each terminal pleopod:	3–4	5	5	8	8	8	3	5	.
Frontal region of carapace–submedian:	spines long	lobes round.	lobes round.	spines long	lobes promnt.	spines long	lobes round.	lobes round.	.
–rostrum:	long, horiz.	long, horiz.	short, deflect.	obtuse	obtuse	obtuse	long, deflect.	long, deflect.	.
Carapace, each protogastric region with:	spine	cristate tubercle	?tubercle	–	long proc.	setae	–	carina	.
orbital region with:	–	–	–	a spine	–	setae	–	–	.
cardiac region with:	long spine	long spine	obtuse process	–	long spine	–	high tubercle	–	.
Spines on abdominal segments:	–	–	?–	+	–	+	–	–	.
Processes or spine, 1st ped. sgmt ant:	–	+	?–	+	+	.	–	+	.

1 Christiansen, 1973; 2 ZII and megalopa after Lebour, 1927, 1928; 3 Lebour (1927) states these are present; they have not been detected in material examined; 4 based on *M. rostrata* and *M. tenuirostris* material: 5 after Bocquet, 1954; 6 based on *E. spinosa* material; 7 based on *P. armata* material: 8–14 Mediterranean ZI *P. tetraodon* figured by Heegaard (1963) with 8: a cleft; 9: innermost longest; 10: absent; 11: 1,2,1; 12: 0; 13: ?0, 2 + 1; 14: 2 + 3: 15 known only from ZII after Rice, 1980.

Provisional key to the larvae of N.E. Atlantic Oxyrhyncha

Zoeae

1 Carapace lateral spines present 2

– Carapace lateral spines absent 5

2 Carapace with a group of 5 lateral spines on each side . . . . ?***Dorynchus thomsoni*** Thomson, (Williamson, 1960).

– Carapace with one lateral spine on each side 3

3 Telson medio-lateral margin strongly concave or medially cleft; middle pair of medio-lateral setae longest; each telson furca with one dorsal and one (rarely 2) lateral spines; 3rd abdominal segment with dorso-lateral process 4

– Telson medio-lateral margin not concave or cleft; medio-lateral setae of equal length; each telson furca without a dorsal spine, one lateral spine present; 3rd abdominal segment without dorso-lateral process . . . . ***Rochinia carpenteri*** Thomson, (Ingle, 1979).

4 Carapace dorsal spine much longer than carapace length; abdominal posterio-lateral process very long; 2nd maxilliped basis with 4 setae; each furca of telson with one lateral spine . . . . ***Hyas coarctatus*** (Leach), ***H. araneus*** (Linnaeus), (Christiansen, 1973).

– Carapace dorsal spine, at the most, slightly longer than carapace length; abdominal posterio-lateral processes short; 2nd maxilliped basis with 3 setae; each furca of telson with 2 lateral spines . . . . . . ***Maja squinado*** (Herbst), (Lebour, 1927, 1928).

5 Carapace rostral spine long; each telson furca with a dorsal spine . . ***Eurynome aspera*** (Pennant), (Lebour, 1928). ***E. spinosa*** Hailstone, (see Table 2, footnote).

– Carapace rostral spine small or absent; each telson furca without a dorsal spine . . 6

6 Telson medio-lateral margin strongly cleft, marginal setae in 2 groups; maxillule endopod* with 0 + 3–4 setae; abdominal posterio-lateral spines long 7

– Telson medio-lateral margin not cleft, marginal setae not in 2 groups; maxillule endopod with 1 + 6 setae; abdominal posterio-lateral spines short . . . . †***Pisa armata*** (Latreille), (Ingle & Clark, 1980).

7 Lateral spine of each telson furca very long (about $\frac{1}{3}$ length of furca and exceeding $\frac{1}{2}$ maximum width of telson) . . . . ***Achaeus cranchii*** Leach, (Bocquet, 1954).

– Lateral spine of each telson furca short, never reaching $\frac{1}{3}$ length of furca 8

8 Lateral spine of each telson furca large; middle medio-lateral seta of telson not longest; maxillule endopod with 0 + 4 setae ***Inachus dorsettensis*** (Pennant), ***I. phalangium*** (Fabricius), ***I. leptochirus*** Leach, (Clark, 1980).

– Lateral spine of each telson furca small; middle medio-lateral seta of telson longest; maxillule endopod with 0 + 3 setae ***Macropodia rostrata*** (Linnaeus), ***M. tenuirostris*** (Leach), (see p. 211), ***M. deflexa*** Forest (Lebour, 1928).

Megalops

1 Abdomen composed of 5 segments (excluding telson); 4 pairs of pleopods, terminal pair with 8 setae on exopod 2

– Abdomen composed of 6 segments (excluding telson); 5 pairs of pleopods, terminal pair with 3–5 setae on exopod 4

2 Dorsal margins of abdominal segments without spinules; carapace submedian spines not developed ***Macropodia rostrata*** (Linnaeus), ***M. tenuirostris*** (Leach) (see p. 211), ***M. deflexa*** Forest (Lebour, 1928).

– Dorsal margins of abdominal segments with small spinules; carapace submedian spines well developed 3

3 Orbital spines present ***Inachus dorsettensis*** (Pennant), ***I. phalangium*** (Fabricius), ***I. leptochirus*** Leach, (Clark, 1980).

– Orbital spines absent . . . . ***Achaeus cranchii*** Leach, (Bocquet, 1954).

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*Not known for *Achaeus cranchii;* †Heegaard's (1963) description of zoea I of *Pisa tetraodon* differs considerably from that of *P. armata* (see Table 2, footnote) and is excluded from this present key.

4 Carapace submedian spines present
. . . . . **Hyas coarctatus** (Leach), **H. araneus** (Linnaeus), (Christiansen, 1973).
– Carapace submedian spines absent 5

5 First peduncular segment of antenna without a distal process; exopod of each terminal pleopod with 3 setae
. . **Eurynome aspera** (Pennant), (Lebour, 1928), **E. spinosa** Hailstone, (see Table 2, footnote).
– First pedunular segment of antenna with an obtuse process or spine; exopod of each terminal pleopod with 5 setae. 6

6 A stout cardiac spine on carapace . . . **Rochinia carpenteri** (Thomson), (Ingle, 1979).
– Without a cardiac spine on carapace. 7

7 Rostral spine well developed; each protogastric region with a carina; exopods of 1st–4th pereiopods with 10 setae . . . . . **Pisa armata** (Latreille), (Ingle & Clark, 1980).
– Rostral spine minute; each protogastric region with (at the most) a tubercle; exopods of 1st–4th pereiopods with 8 setae . . . **Maja squinado** (Herbst), (Lebour, 1927, 1928).

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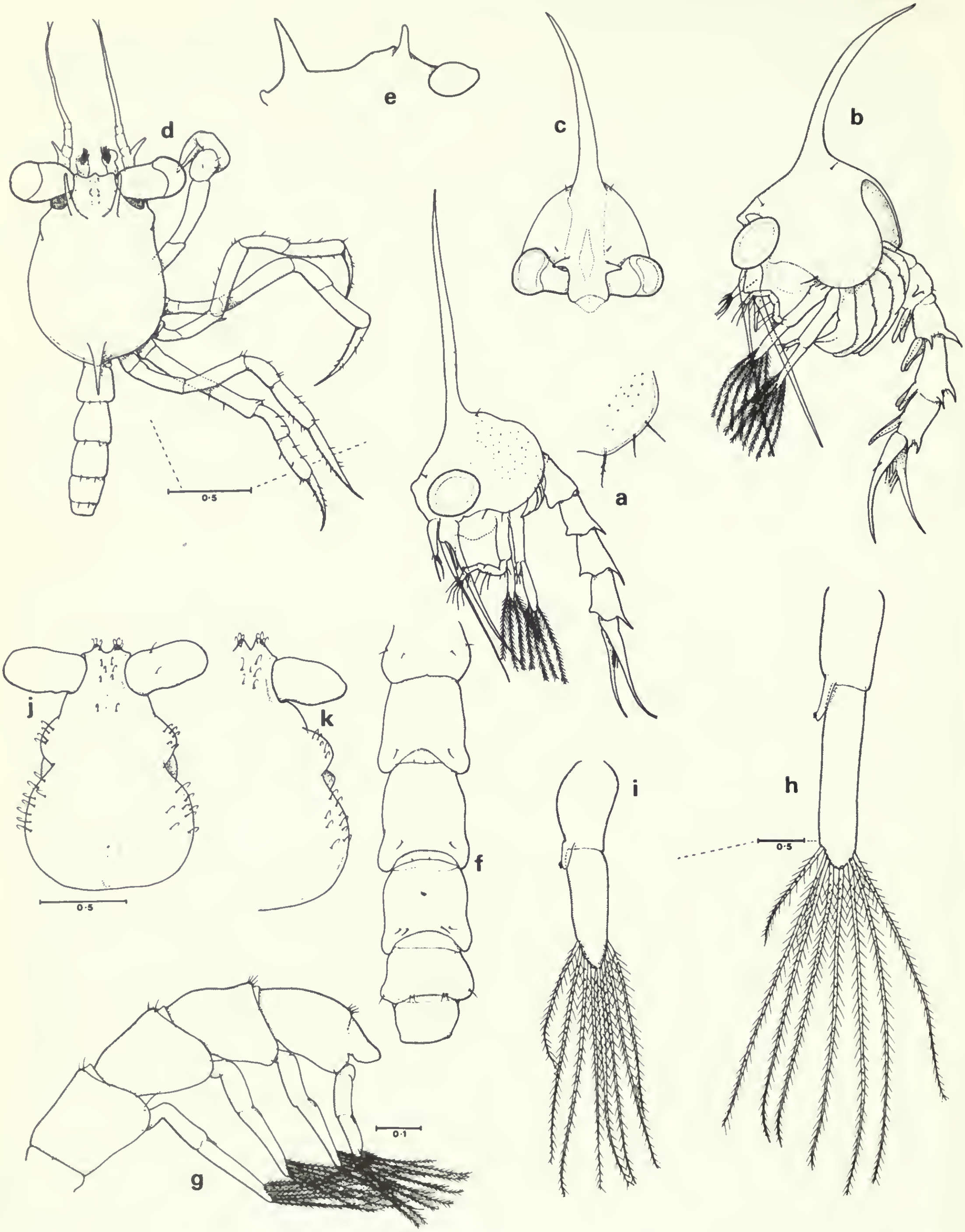

Fig. 1 *Macropodia rostrata* (L.): a, b zoea I & II respectively from lateral aspects; c zoea II carapace and eyes from frontal aspect; d megalopa from dorsal aspect and e lateral aspect of carapace and eye; f dorsal and g lateral aspect of megalopal abdomen; h first and i fourth left megalopal pleopods; carapace of the first crab from j–Isle of man cf. with k–Tunisian waters.

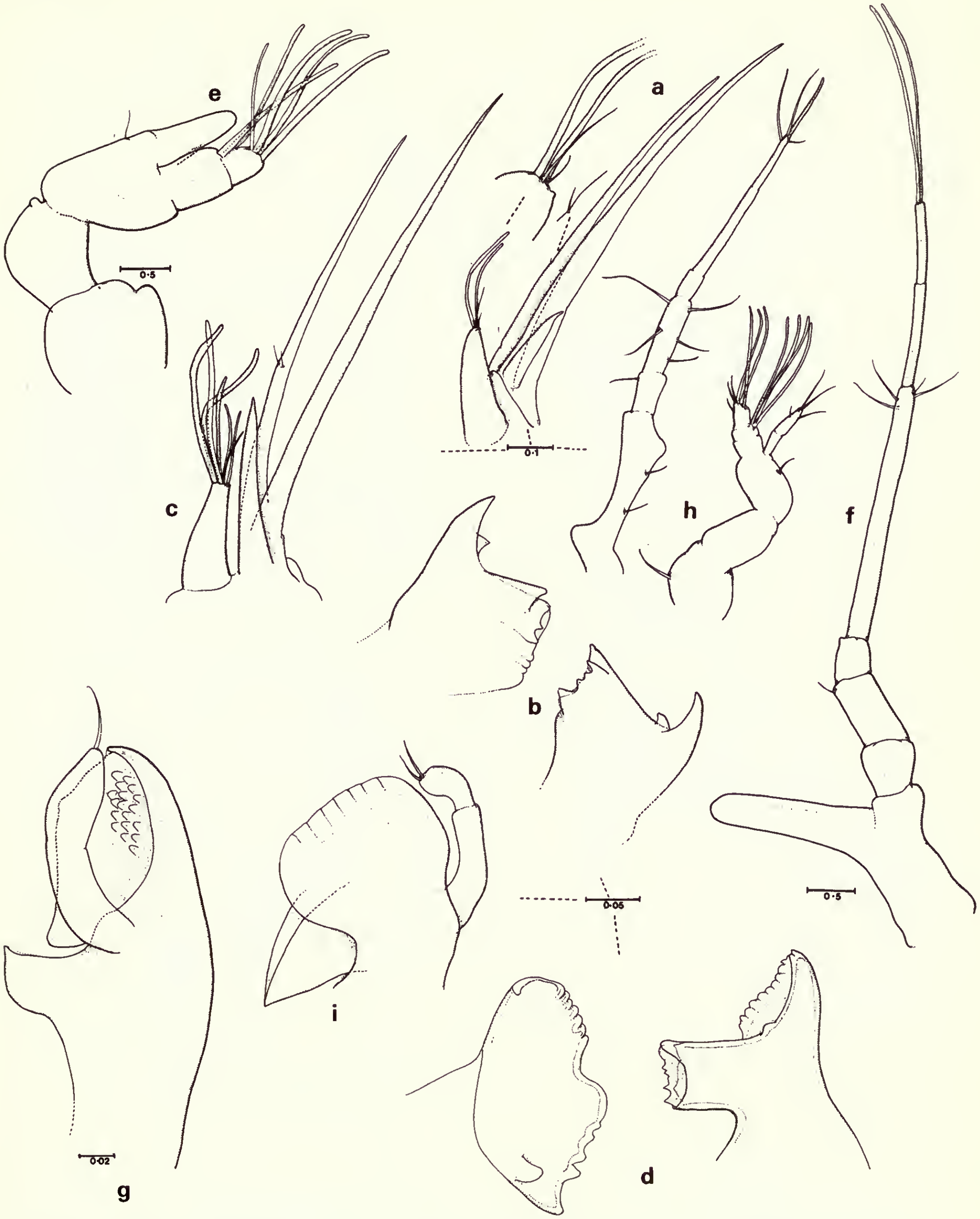

Fig. 2 *Macropodia rostrata* (L.): zoea I, a antennule and antenna, b mandible; zoea II, c antennule and antenna, d mandible; megalopa, e antennule, f antenna, g mandible; first crab, h antennule & antenna, i mandible.

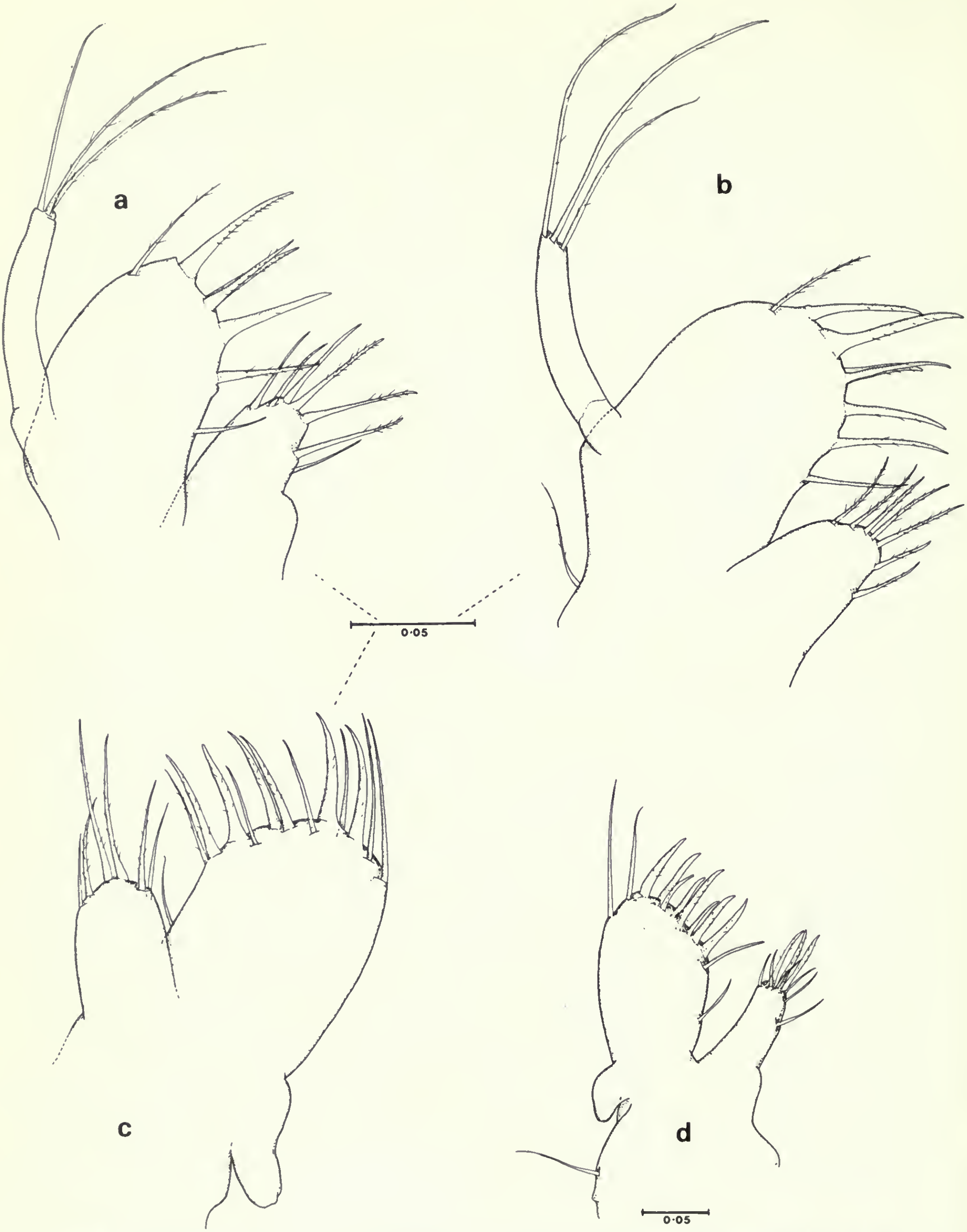
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Fig. 3 *Macropodia rostrata* (L.): maxillule of– a zoea I; b zoea II; c megalopa; d first crab.

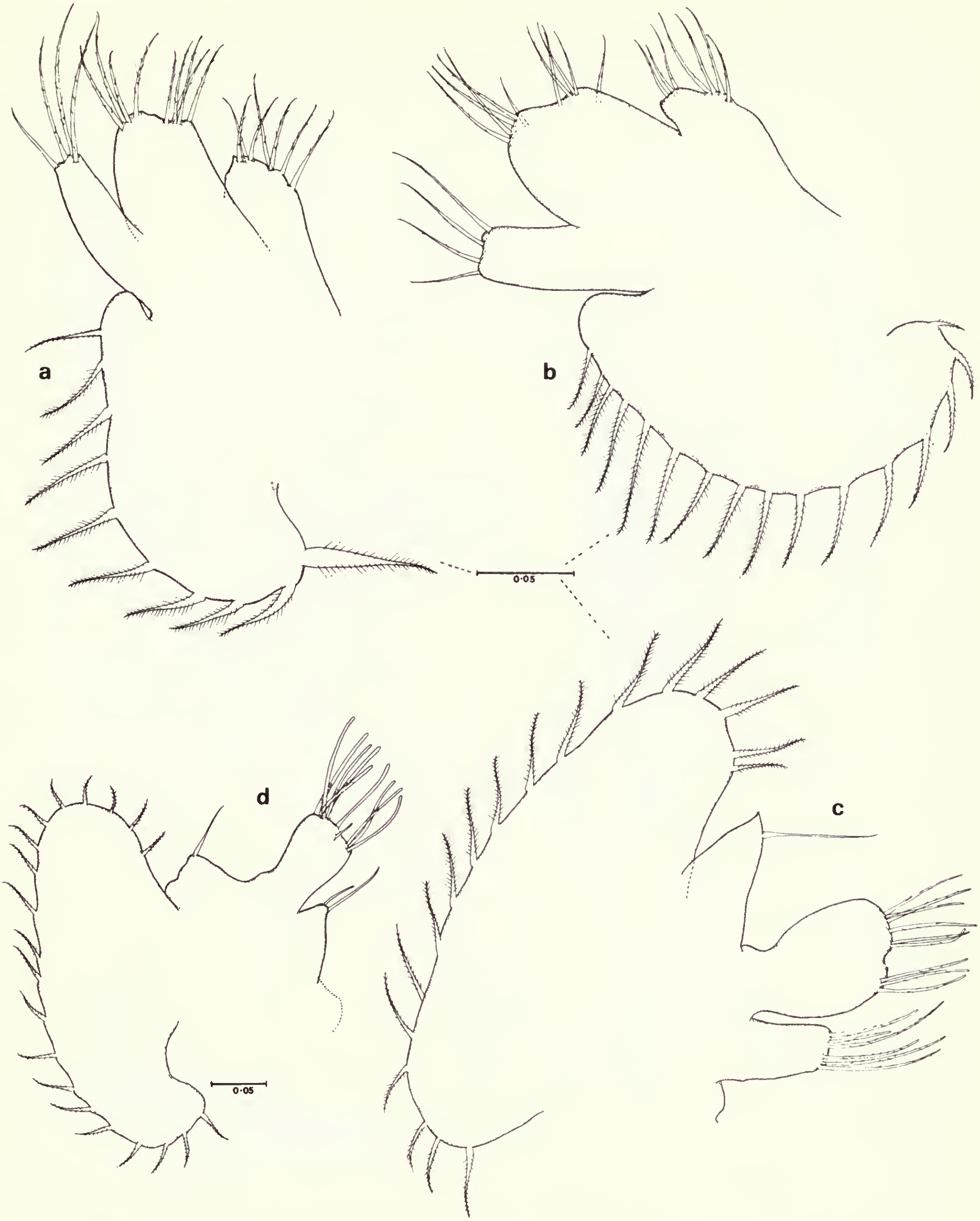

Fig. 4 *Macropodia rostrata* (L.): Maxilla of– a zoea I; b zoea II; c megalopa; d first crab.

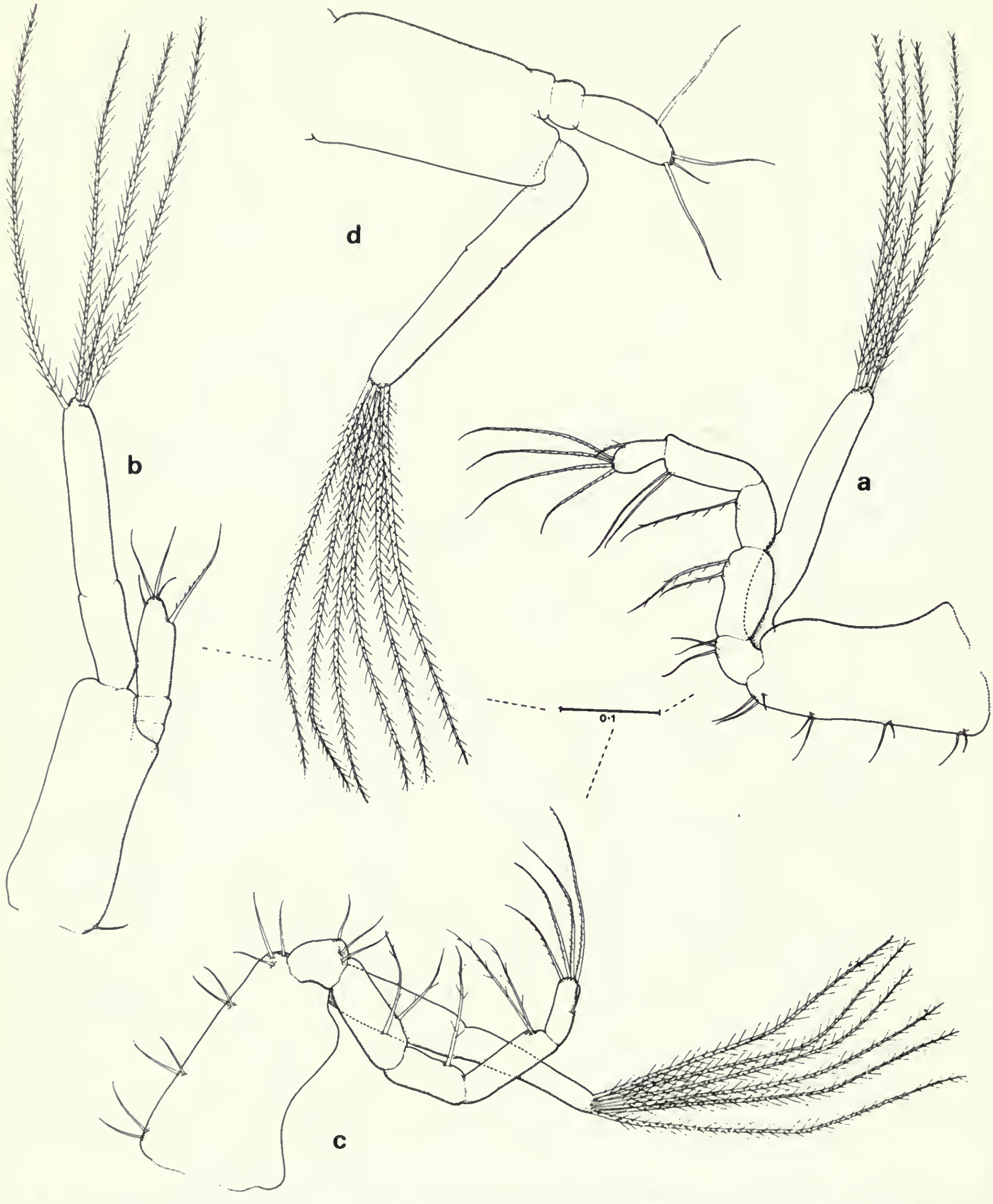

Fig. 5 *Macropodia rostrata* (L.): a & b 1st & 2nd maxillipeds of zoea I; c & d 1st & 2nd maxillipeds of zoea II.

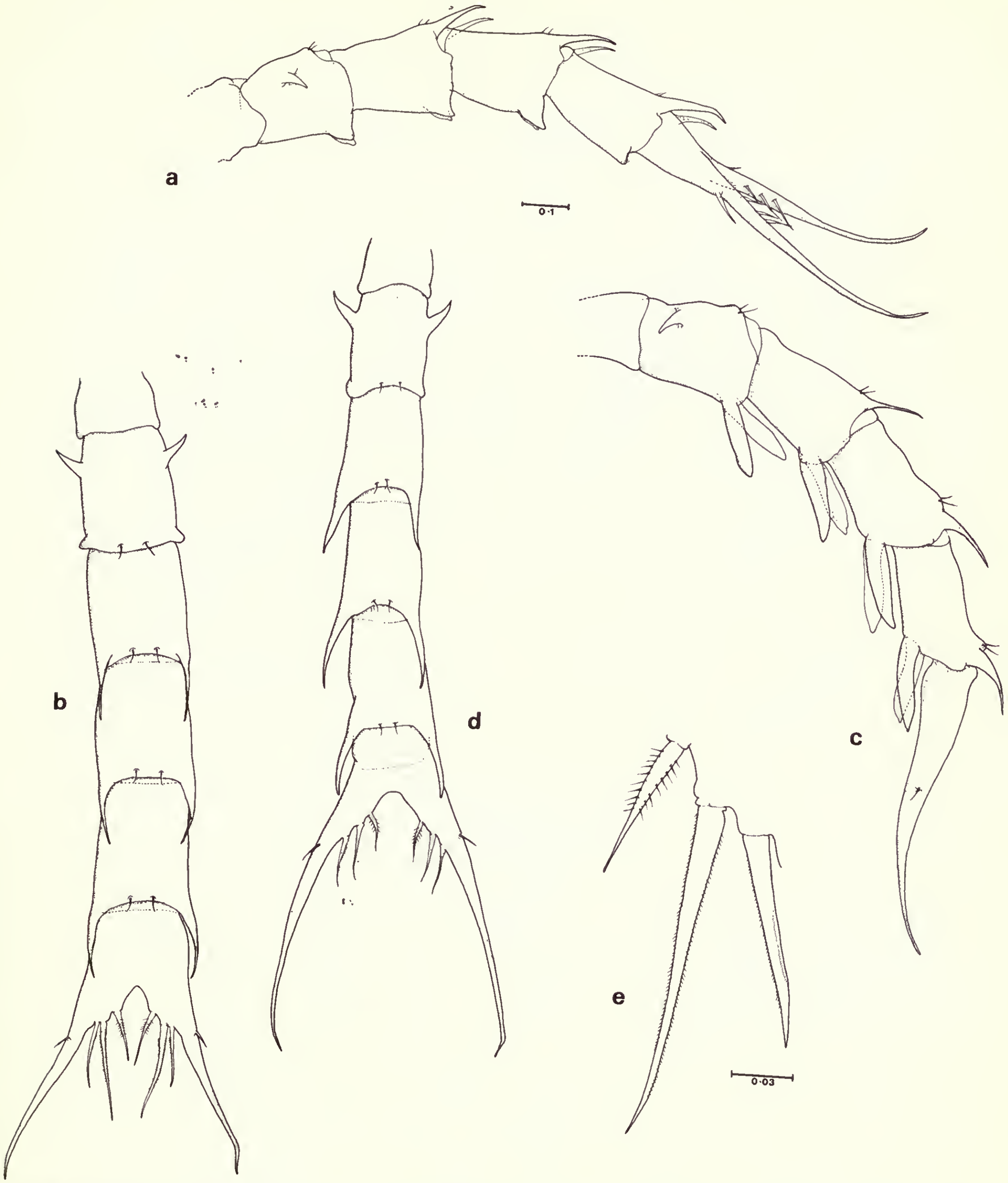

Fig. 6 *Macropodia rostrata* (L.): abdominal segments and telson a & c lateral, b & d dorsal aspects of– a, b zoea I; c, d zoea II; e spines on right medio-lateral margin of telson of zoea I.

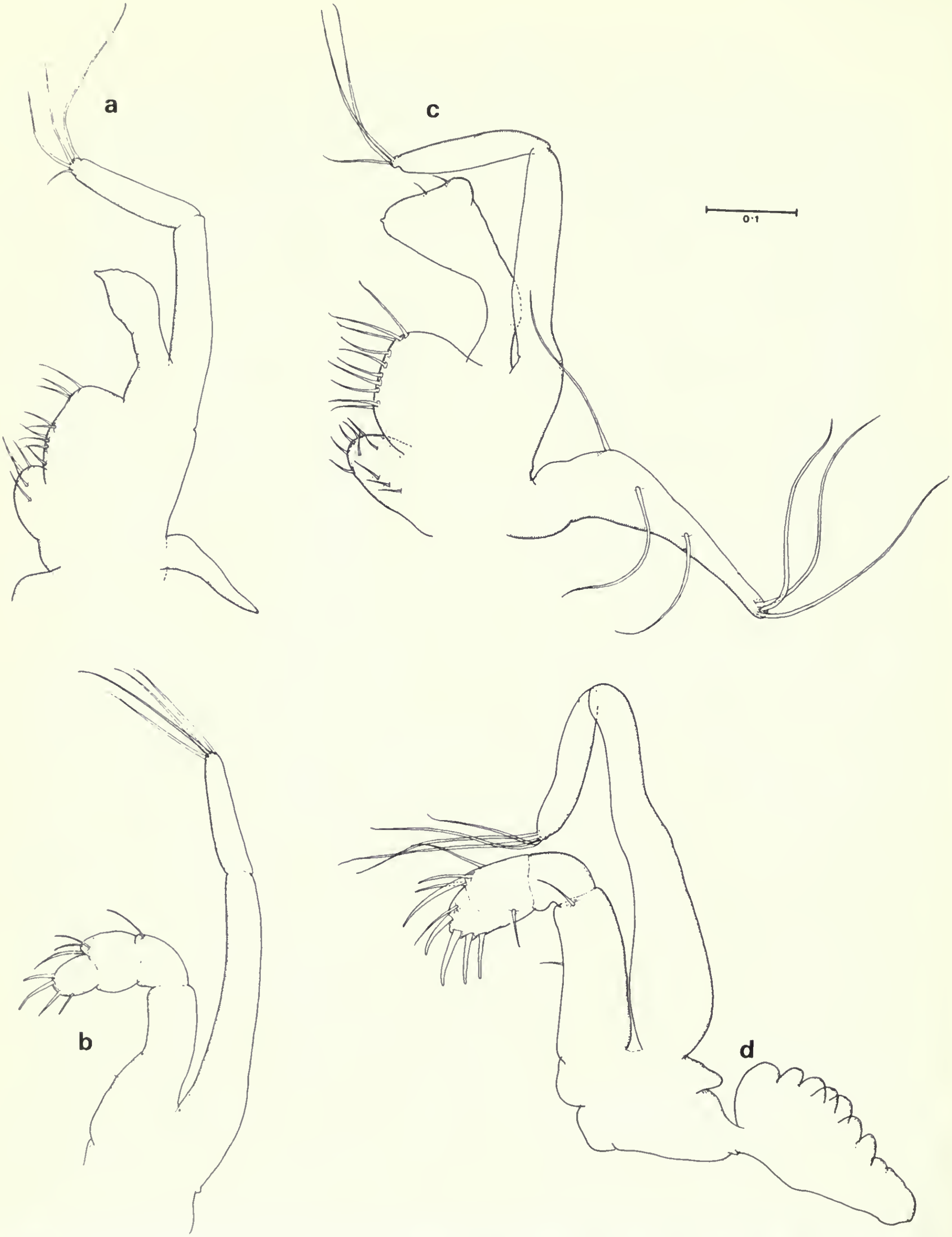

Fig. 7 *Macropodia rostrata* (L.): 1st (a, c) & 2nd (b, d) maxillipeds a, b megalopa; c, d first crab.

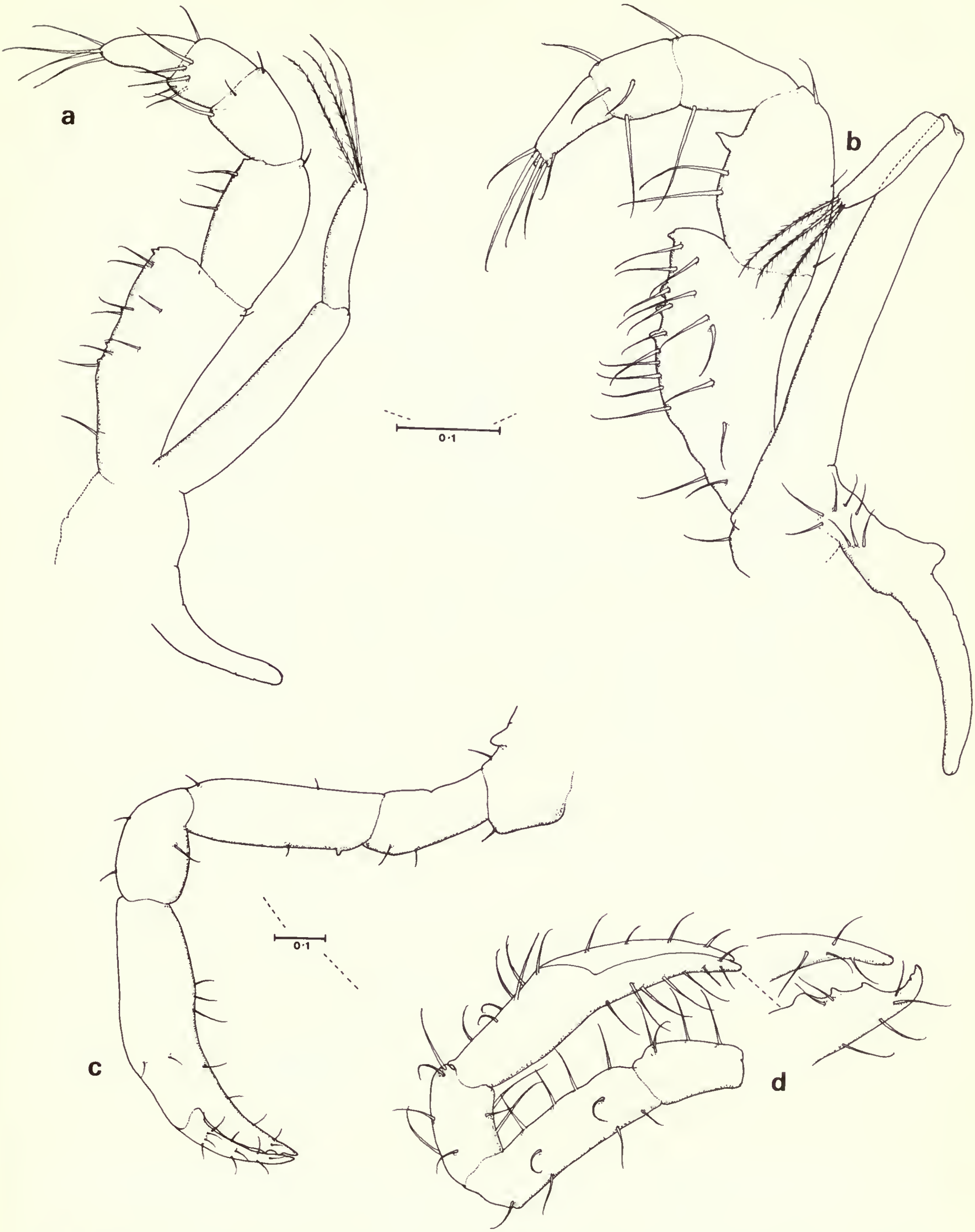

Fig. 8 *Macropodia rostrata* (L.): 3rd maxilliped– a megalopa; b first crab; cheliped– c megalopa; d first crab.

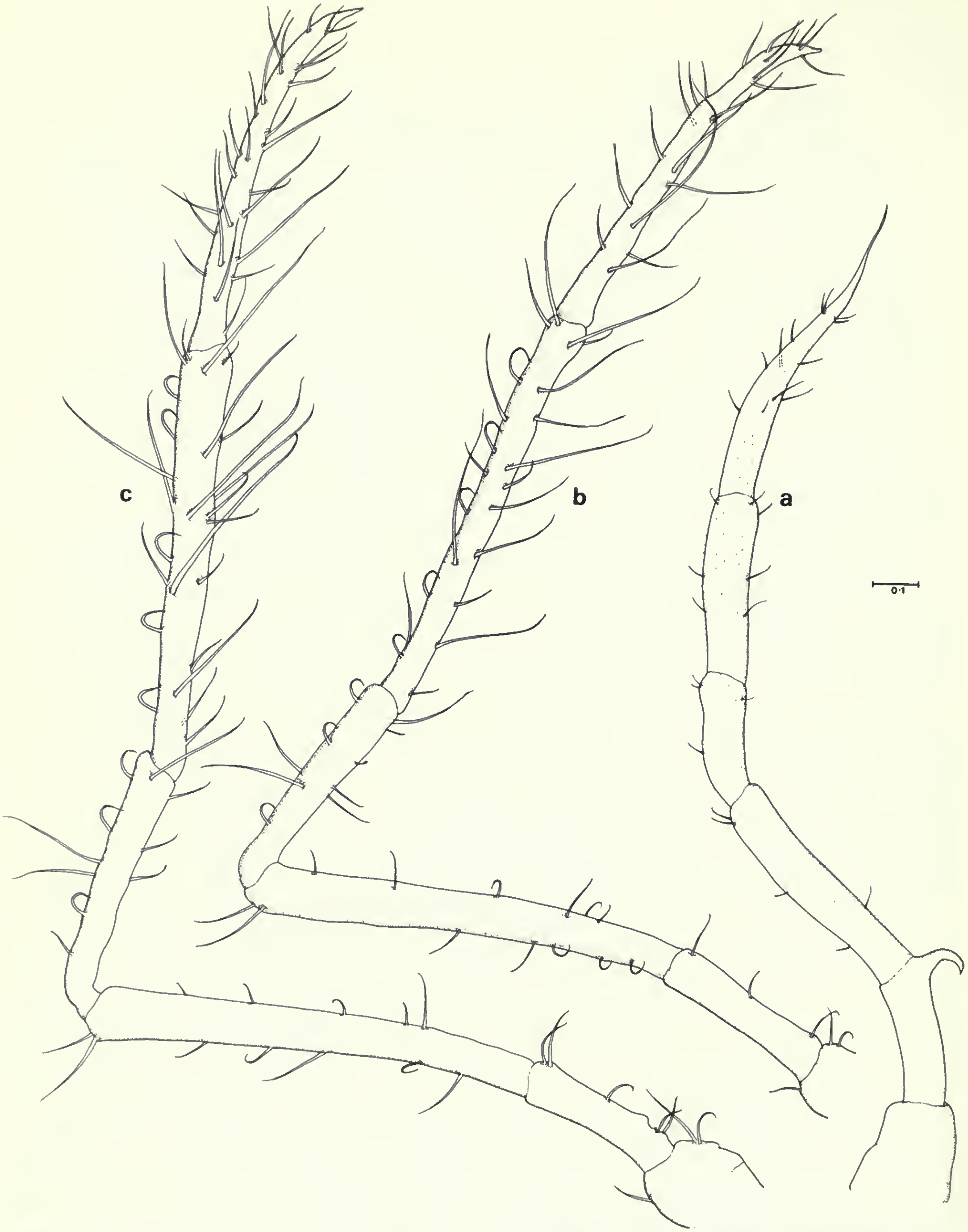

Fig. 9 *Macropodia rostrata* (L.): a 2nd pereiopod of megalopa; b, c 2nd & 3rd pereiopods of 1st crab.

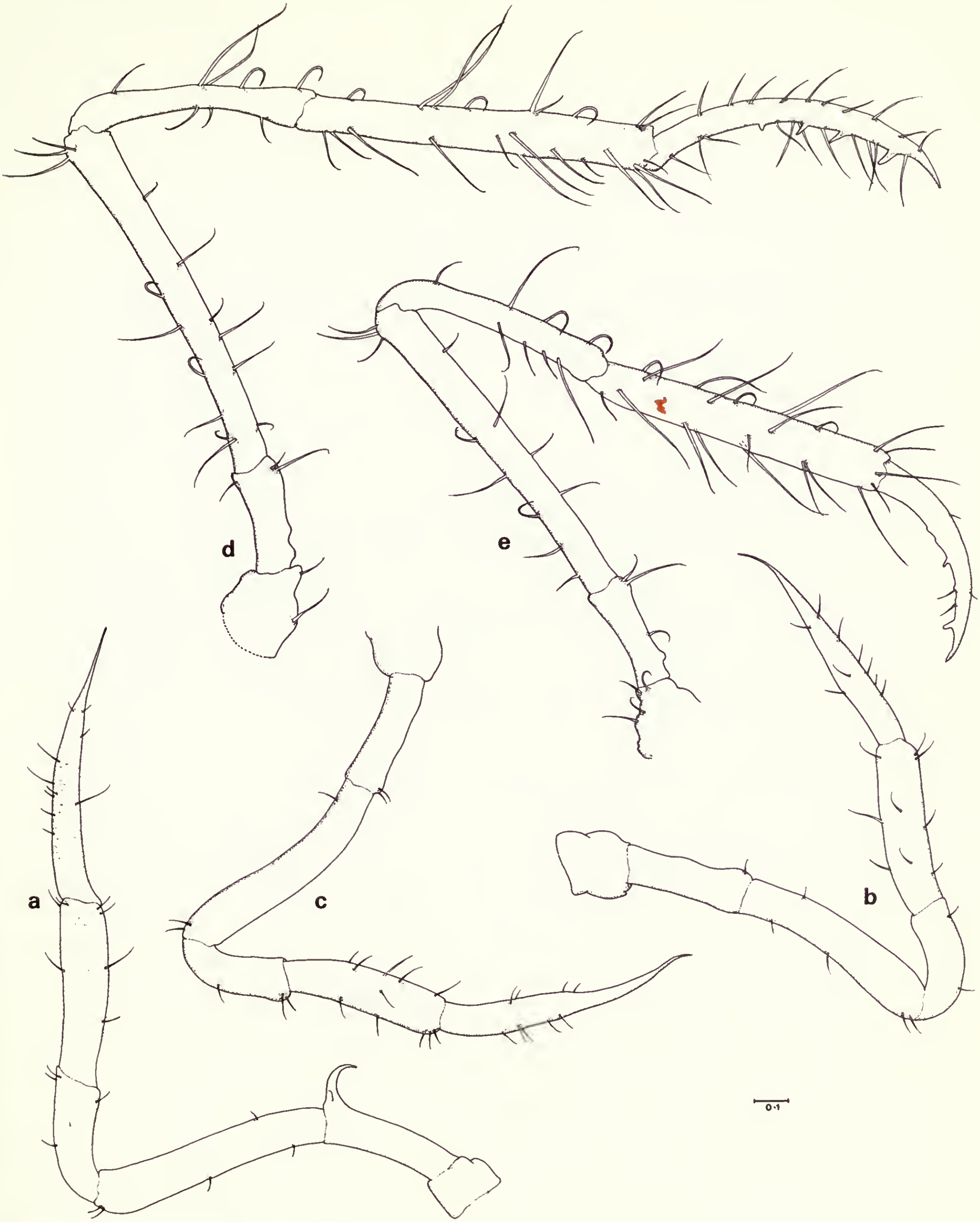

Fig. 10 *Macropodia rostrata* (L.): a–c 3rd–5th pereiopods of megalopa; d & e 4th & 5th pereiopods of first crab.

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New species of marine nematodes from Loch Ewe, Scotland

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Z. N. Zhang

Shandong College of Oceanography, Qingdao, Shandong Province, People's Republic of China[1]

Introduction

During an investigation of the shallow sublittoral nematode fauna off a small sandy bay in Scotland one of us (Z.N.Z.) encountered a number of previously undescribed species. These were studied in detail at the British Museum (Natural History) and we here present descriptions of six of the more interesting species: *Gerlachius novusetosus, Catanema macintyrei, Catanema smo, Ceramonema yunfengi, Acantholaimus ewensis* and *Rhips paraornata.* A new diagnosis is given for the subfamily Gerlachinae Andrassy, 1976. The genus *Robbea* Gerlach, 1956 is synonymized with *Catanema* Cobb, 1920; a new generic diagnosis and a key to the species is given. Keys are also provided for the genera *Ceramonema* Cobb, 1920 and *Acantholaimus* Allgen, 1933. Several other minor nomenclatorial changes are suggested. Species belonging to these five genera have not been found previously in British waters and *Rhips* Cobb, 1920 has not previously been recorded from Europe.

Material and methods

All specimens came from the same place; sublittoral sand in 3 m of water off 'north beach', Firemore Bay, Loch Ewe, Wester Ross, Scotland. Detailed descriptions of the bay and its fauna can be found in Steele & Baird (1968), McIntyre & Eleftheriou (1968) and McIntyre & Murison (1973). The glycerine mounted specimens were studied using a Leitz Ortholux II microscope equipped with differential interference contrast facility. All drawings were made using a drawing tube. The formulae used for the dimensions are a modification of Filipjev's (1918) formula and the de Man ratios, as described in Platt (1973). The abbreviations 'S' and 'V' are the spicule length and the relative position of the vulva respectively. The abbreviations 'a.b.d.' and 'c.d.' are the anal (or cloacal) body diameter and corresponding (body) diameter. Type material has been deposited at the British Museum (Natural History).

Systematic descriptions

The classification follows that given in Gerlach & Riemann (1973).

Subfamily **GERLACHINAE** Andrassy, 1976

DIAGNOSIS. Meyliidae. Cuticle smooth or feintly striated. Amphids circular, lightly cuticularised or invisible. Testes paired, opposed. Ovaries reflexed.

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Discussion. Andrassy (1976) erected the genus *Gerlachius* to distinguish *Meylia lissa* Gerlach, 1956 from the other two species of the genus, *M. alata* Gerlach, 1956 and *M. spinosa* Gerlach, 1956. According to Andrassy, *Gerlachius* is characterized by its smooth cuticle and invisible amphids: the specimens described below are similar to *G. lissus* in many respects apart from these two main generic characters. However, the cuticle in *G. novusetosus* sp. nov. was observed under interference contrast and can otherwise be seen only as feintly striated so that this feature may have been overlooked in *G. lissus.* Likewise, the amphid may have been overlooked, since in the male *G. novusetosus* sp. nov. it was difficult to distinguish. Therefore, at this stage we prefer simply to widen the subfamily and genus diagnosis to permit forms with a smooth cuticle without amphids until these animals become better known.

The subfamily Gerlachinae can now be distinguished from Meyliinae since the ovaries are outstretched in the latter (Lorenzen, 1981) but reflexed in the former.

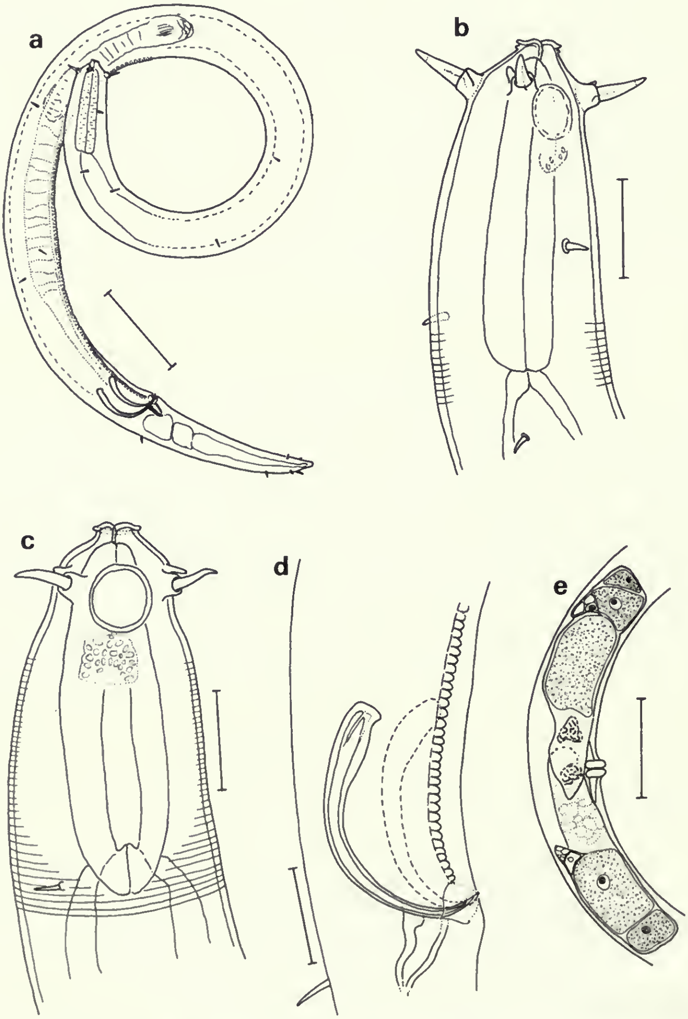

Fig. 1 *Gerlachius novusetosus*: (a) whole body of ♂; (b) head of ♂; (c) head of ♀; (d) copulatory apparatus of ♂; (e) ♀ reproductive system. Bar scales: a,e = 40 μm; b,c,d = 10 μm.

Gerlachius novusetosus sp. nov.

Fig. 1

MATERIAL STUDIED. Holotype: ♂ BM(NH) 1981.4.10.
Allotype: ♀ BM(NH) 1981.4.11.

DIMENSIONS.

Holotype ♂: $\frac{-\quad 34\quad M\quad 433}{11\quad 18\quad 22\quad 17}$ 505 μm; a=23; b=14·9; c=7·0; S=31 μm

Allotype ♀: $\frac{-\quad 34\quad 280\quad 463}{12\quad 22\quad 27\quad 17}$ 515 μm; a=19; b=15·1; c=9·9; V=54%

DESCRIPTION. Short, relatively stout body. Cuticle feintly striated. Short 2·5–3·5 μm sublateral somatic setae present (Fig. 1a): they are not bilaterally symmetrical. Four 5·5 μm submedian cephalic setae (R3?) seated on short 1·5 μm peduncles. A short stout additional seta, 2–2·5 μm long, is associated with each cephalic seta positioned as shown in Fig. 1b, c. Amphid round, not strongly cuticularised, 7 μm long and 6·5 μm wide in female (male amphid less distinct but about 5·5 μm long). Posterior to the amphid there is a subcuticular reticulate structure (Fig. 1c) of unknown function. Buccal cavity absent. Oesophagus short, without a bulb. Tail conical, 3–4 a.b.d. Three conspicuous caudal glands lying entirely in the tail.

Spicules curved and slightly cephalate proximally: chord length 23 μm, arc length 31 μm. Gubernaculum has a dorso-caudally directed apophysis. Anterior to cloaca the cuticle striations are thickened ventrally to produce a longitudinal row of contiguous pegs which extends about 190 μm from the cloaca (Fig 1a, d). Testes paired, opposed.

Vulva cuticularised and prominent. Ovaries paired, opposed, reflexed.

DIFFERENTIAL DIAGNOSIS. *Gerlachius novusetosus* sp. nov. differs from the only other species, *G. lissus* (Gerlach, 1956) in having four short additional cephalic setae, shorter cephalic setae (5·5 μm vs 15 μm), shorter oesophagus (b = 15 vs 7) and precloacal cuticular differentiation.

DISCUSSION. The reticulate organ posterior to the amphid and the four additional pegs alongside the cephalic setae have not been reported previously. However, this whole group of what appear to be primitive desmoscolids are poorly known, the only other records being *G. lissus* (Gerlach, 1956), *Meylia alata* Gerlach, 1956 and *M. spinosa* Gerlach, 1956; all from Kiel Bay.

CATANEMA Cobb, 1920

Robbea Gerlach, 1956 syn. nov.

The genus *Catanema* was originally described by Cobb, 1920 to accommodate *C. exile* from Jamaica, a male specimen with fine cuticle striations, narrow buccal cavity 'enclosed in a swelling', seven pairs of subventral postcloacal tubular organs, proximally cephalate spicules and a large dorso-caudally directed gubernacular apophysis. Three further species have subsequently been assigned to the genus: *C. cobbi* Inglis, 1968, with ten pairs of subventral postcloacal organs, cephalic cuticle 'modified into blocks' and a dorsally directed gubernacular apophysis; *C. porosum* Hopper & Cefalu, 1973, with five pairs of subventral postcloacal organs; *C. gerlachi* Hopper & Cefalu, 1973. This last species was a new name for a specimen from the Maldive Islands originally described by Gerlach (1963*a*) under the name *Eubostrichus exilis* (Cobb, 1920). However, as Hopper & Cefalu (1973) point out, Gerlach (1963*a*) makes no mention of the buccal bulb so characteristic of this genus and the gubernaculum lacks the prominent apophysis, which in Gerlach's specimen is thin and lies almost parallel to the spicules.

Hopper & Cefalu (1973) decided to keep this record within the genus *Catanema*. However, we feel that it is more probable that Gerlach would not have overlooked a buccal bulb if it were present (having already described nematodes with this character, e.g. *Robbea caelestis* Gerlach, 1956) so we transfer this species back to *Eubostrichus*, becoming *Eubostrichus gerlachi* (Hopper & Cephalu, 1973) comb. nov. *Eubostrichus* is characterized as having modified 'porids' on the tail (Hopper & Cefalu, 1973: porids = tubular setae serving as outlets for glands): Gerlach (1963 p. 95) depicts similar structures in both *E. parasitiferus* Chitwood, 1936 and his *E. exisis* (= *E. gerlachi*) from the Maldive Islands and both species have similarly shaped gubernacula.

In 1956, Gerlach erected the genus *Robbea* for a male specimen from Brazil, considering that the muscular buccal bulb distinguished the taxon from all other related genera. Although the type, *R. caelestis*, is certainly depicted as having a very prominent buccal bulb, some species described subsequently seem to have somewhat less prominent bulbs, depicted as similar to those described for *Catanema*. This being so, we propose to synonomize *Robbea* with *Catanema* so that *Catanema* now also includes the following species: *C. caelestis* (Gerlach, 1956), *C. gallica* (Vitiello, 1974) and *C. tenax* (Gerlach, 1963*b*). *C. gerlachi* (Boucher, 1975) was described from a female only: since male characters are of importance in this taxon, and despite the fact that *C. gerlachi* seems to be unique in the length of its subcephalic setae, we prefer to treat it as a *species inquirenda*.

In proposing this synonomy, there remains two main points to discuss: the amphid of the type and the presence of subventral tubular supplements on the male tail. In Cobb's (1920) description of the type, *C. exile*, he describes the amphids as 'minute labial tubes'. However, he also states that they were 'forward-pointing . . . difficult to see'. A similar anterior position was found in *C. smo* sp. nov. described here and we feel confident that Cobb misinterpreted what were spiral, albeit minute, amphids. Cobb (1920) also depicted the type with seven prominent pairs of subventral tubular supplements on the tail, similar to the modified porids found in *Eubostrichus*. We cannot be sure whether these supplements, found in *C. exile, C. cobbi* and *C. porosum* are homologous with the stout caudal setae described in *C. caelestis, C. gallica, C. tenax* and the two new species described here. However, their presence or absence seems to be no more significant a reason for suggesting a generic split than say the presence of huge cervical suckers in *C. tenax* or the reticulate head of *C. cobbi*. Therefore, we consider the presence or absence of caudal supplements as a variable infrageneric character.

Finally, we would comment on the arrangement of setae on the head. Inglis (1968) described 6 + 4 cephalic setae, the lateral components of the R_2 circle being 'markedly dorsal' in position (although, according to the direction of the amphid spiral, he mistook ventral for dorsal). However, in most species, there are four prominent setae, often longer than the others; we judge these to be the four R_3 sensilla. The six R_2 sensilla are small in size, often not depicted but can be clearly seen in the two species described here. If so, the R_1 sensilla must be reduced to papillae and may require SEM to resolve. In all species, each R_3 sensillum seems to be accompanied by a more medially situated subcephalic seta, which may be at about the same level as the R_3 sensilla as in *C. tenax* or more posterior as in *C. caelestis*. It is these which Inglis (1968) called the four cephalic setae. In addition to these subcephalic setae, there are others on the cephalic capsule which, according to the several specimens of each species described here, seem to be quite stable in position. Most species, including *C. smo* sp. nov., have setae located either side of the base of the amphid. In at least *C. cobbi, C. macintyrei* sp. nov. and *C. tenax* there are additional setae in specific locations. For example, in *C. cobbi* there is a pair of setae either side of the base of the amphid and an additional seta associated with each ventral subcephalic seta. In *C. macintyrei* sp. nov. there is a seta close behind each subcephalic seta, a small seta associated with each ventral R_3 seta and a seta lying dorsal to the amphid.

We propose the following generic diagnosis: *Catanema*. Desmodoridae. Stilbonematinae. Elongated body. Cuticle finely striated posterior to cephalic capsule and in life covered with coccoid blue-green algae. Cephalic capsule may appear reticulate or feintly punctated. Four anteriorly directed R_3 cephalic setae and four subcephalic setae. Additional subcephalic setae may be present on the cephalic capsule. Spiral amphid. Buccal cavity minute and funnel-shaped leading to a muscular buccal bulb. Oesophagus narrow, terminating in a rounded posterior bulb. Spicules curved and proximally cephalate. Gubernaculum with a solid dorsally or dorso-caudally directed apophysis. Single outstretched testis. Subventral pairs of tubular organs may be present on the tail. Tail conical.

TYPE SPECIES. *Catanema exile* Cobb, 1920

Key to the species of *Catanema*

1 Ventral suckers present in oesophageal and post-oesophageal region **C. tenax** (Gerlach, 1963) comb. nov.
syn. *Robbea tenax* Gerlach, 1963
– Ventral suckers absent 2
2 Cephalic cuticle in conspicuous blocks. 10 pairs subventral caudal supplements **C. cobbi** Inglis, 1968
– Cephalic cuticle smooth or with feint punctations 3
3 Tail tip pointed. 'a' ratio >200. Amphid large (0·7 c.d.) **C. caelestis** (Gerlach, 1956) comb. nov.
syn. *Robbea caelestis* Gerlach, 1956
– Tail tip rounded. 'a' ratio <200 4
4 Amphid situated far anterior so that subcephalic and subamphidal setae are on the same level. 7 pairs subventral caudal supplements . . . . . . **C. exile** (Cobb, 1920)
– Amphid situated further posterior 5
5 Middle of amphid situated at 10% of length of buccal bulb from anterior . . **C. smo** sp. nov.
– Middle of amphid situated at least 30% of length of buccal bulb from anterior 6
6 Cephalic setae 8 μm long (0·3 c.d. at base of buccal bulb) **C. gallica** (Vitiello, 1974) comb. nov.
syn. *Robbea gallica* Vitiello, 1974
– Cephalic setae > 17 μm long (0·8 c.d. at base of buccal bulb) 7
7 Only 4 subcephalic setae and 4 subamphidal setae between base of amphid and anterior **C. porosum** Hooper & Cefalu, 1973
– Additional subcephalic setae present . . . . **C. macintyrei** sp. nov.

Catanema macintyrei sp. nov.
Figs 2–3

MATERIAL STUDIED. Holotype: ♂$_1$ BM(NH) 1981.5.22.
Allotype: ♀$_1$ BM(NH) 1981.5.23. Paratypes: five males and five females BM(NH) 1981.5.24–29, 31–34.

DIMENSIONS.

Holotype ♂: $\dfrac{-\quad 87\qquad \text{M}\quad 3710}{25\quad 25\qquad 27\qquad 23}$ 3770 μm; a = 142; b = 43; c = 65; S = 47 μm

Allotype ♀$_1$: $\dfrac{-\quad 94\quad 1845\quad 3555}{25\quad 25\qquad 29\qquad 24}$ 3620 μm; a = 125; b = 39; c = 56; V = 51%

♂$_2$: L = 3720 μm; a = 138; b = 37; c = 66; S = 47 μm
♂$_3$: L = 3965 μm; a = 137; b = 42; c = 71; S = 44 μm
♂$_4$: L = 4170 μm; a = 143; b = 47; c = 72; S = 44 μm
♂$_5$: L = 3875 μm; a = 146; b = 45; c = 64; S = 43 μm
♂$_6$: L = 3540 μm; a = 128; b = 41; c = 61; S = 41 μm
♀$_2$: L = 4065 μm; a = 145; b = 47; c = 71; V = 50%
♀$_3$: L = 3720 μm; a = 143; b = 40; c = 69; V = 50%
♀$_4$: L = 4510 μm; a = 161; b = 46; c = 76; V = 52%
♀$_5$: L = 4010 μm; a = 143; b = 47; c = 78; V = 52%
♀$_6$: L = 4530 μm; a = 162; b = 49; c = 79; V = 49%

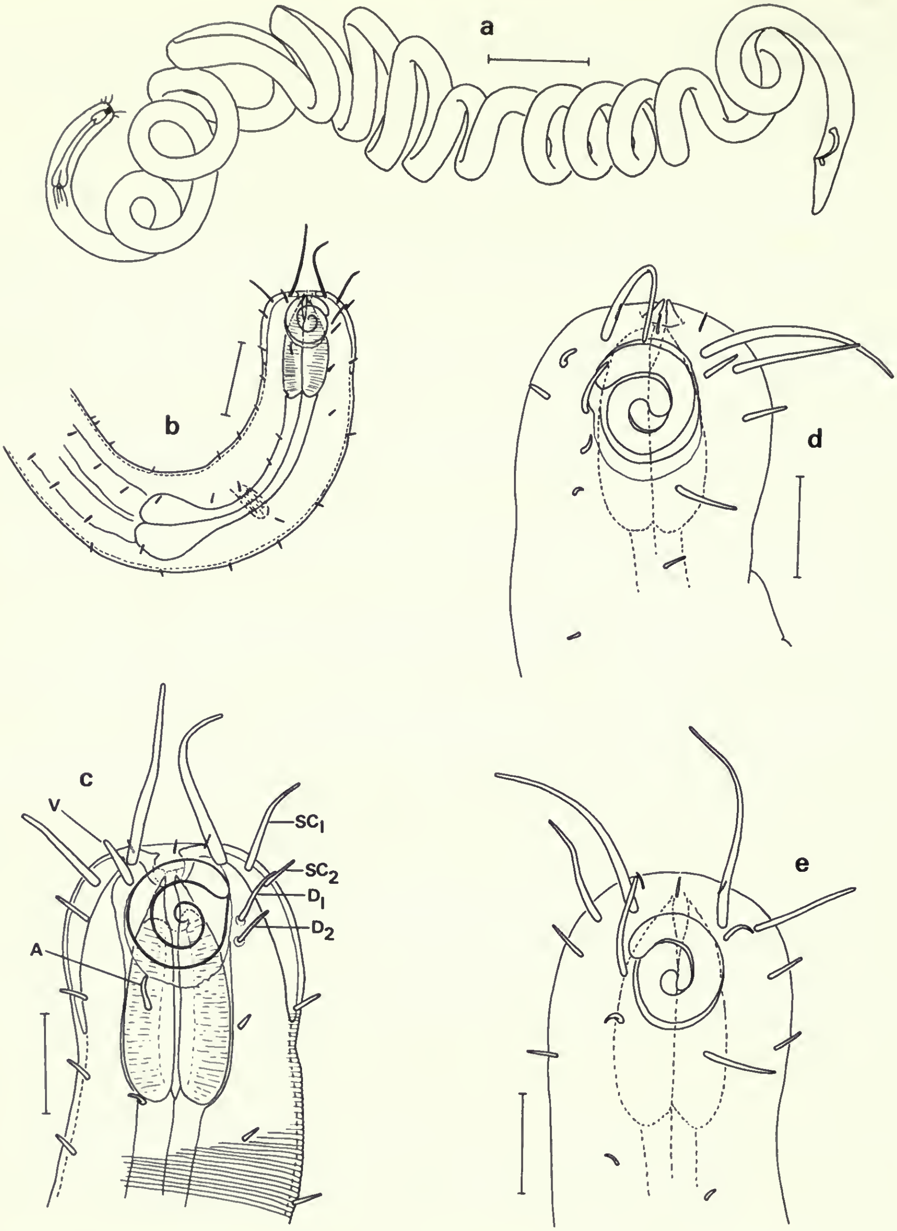

Fig. 2 *Catanema macintyrei*: (a) whole body of ♂$_2$; (b) oesophageal region of ♂$_1$; (c) head of ♂$_1$ (see text for labelling); (d) head of ♂$_7$; (e) head of ♀$_1$. Bar scales: a = 100 μm; b = 30 μm; c–e = 10 μm.

Spicule (S) measurement is the arc. Maximum body diameter used is the average of three measurements along the middle portion of the body.

DESCRIPTION. Cuticle finely striated from the base of the cephalic capsule, but most conspicuous in the oesophageal and immediate post-oesophageal regions. Typically, the cuticle is covered with a coating of coccoid blue-green algae, but this tends to be lost during preservation. One specimen also had two suctorian ectoparasites attached to the middle part

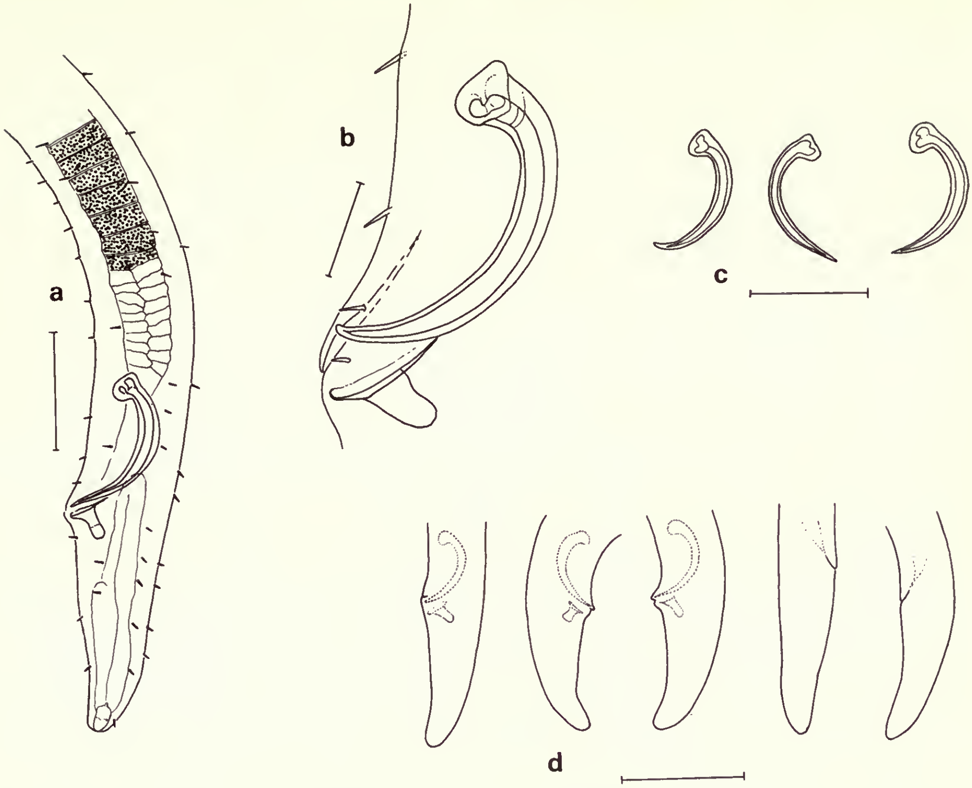

Fig. 3 *Catanema macintyrei*: (a) tail region of ♂$_2$; (b) copulatory apparatus of ♂$_1$; (c) spicules of three different males; (d) tails of three males and two females. Bar scales: a,c = 30 μm; b = 10 μm; d = 50 μm.

of the body. Cuticle bears six files of stout setae throughout the body, but they are particularly conspicuous ventrally in the region just posterior to the oesophagus and in the male, anterior to the cloaca. R_1 sensilla not seen. Six small 1·5–2 μm setose R_2 sensilla. Four 17·5–24 μm R_3 setae, about 80% of the maximum diameter of the cephalic capsule. The head diameter is usually measured at the level of the R_3 sensillae, but they are so far anterior as to make this measurement too inaccurate. Medial and slightly posterior to the R_3 setae are four 11–14 μm subcephalic setae (labelled SC_1 in Fig. 2c). Further posterior are four smaller 6·5–8·5 μm setae (labelled SC_2 in Fig. 2c). In addition, there is one seta just posterior to the ventral R_3 seta (Fig. 2c, V), two level with and dorsal to the middle of the amphid (Fig. 2c, D_1 & D_2) and one ventro-sublateral subamphidal seta (Fig. 2c, A). The disposition of these setae is constant in that each element can be distinguished in the same location in all the specimens, both male and female. Amphid ventrally wound, from outside to centre; 9–10 μm wide. Buccal cavity represented by a narrow funnel in the anterior part of the buccal bulb, the latter being about 23 μm long. Tail conical with a characteristic slight ventral inflection at the tip.

Spicules paired, curved and proximally cephalate: average length 44 μm (arc) or 32 μm (chord). Gubernaculum well cuticularised and dorso-caudally directed. Testis single and outstretched.

Ovaries paired and apparently outstretched.

DIFFERENTIAL DIAGNOSIS. *Catanema macintyrei* sp. nov. can be distinguished from the other species in the genus *Catanema* by the unique disposition of the setae around the head. From the other sympatric species, *C. smo* sp. nov., it can also be distinguished by the larger and slightly more posteriorly situated amphid.

DISCUSSION. This species will be discussed together with the following species.

Catanema smo sp. nov.

Fig. 4

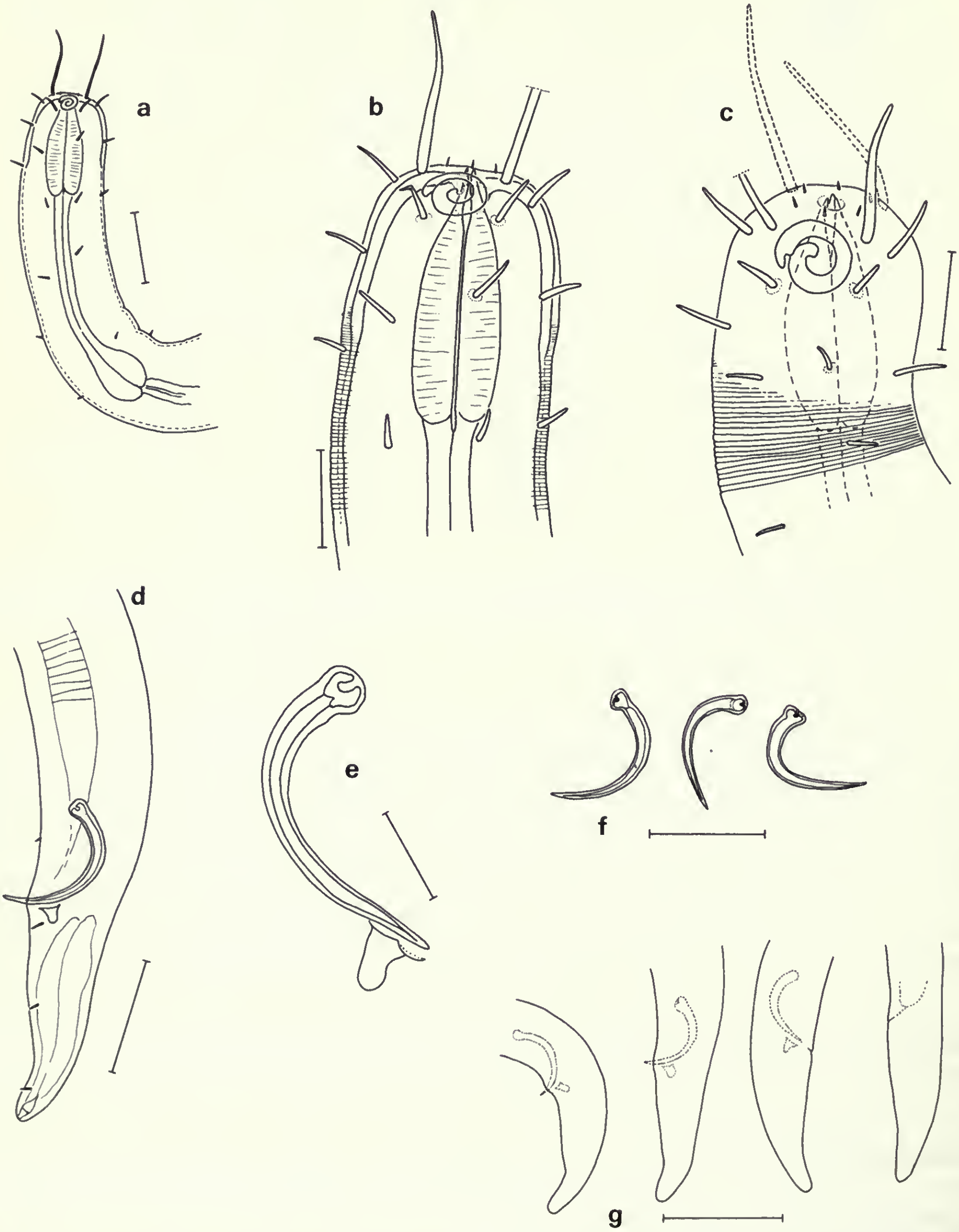

Fig. 4 *Catanema smo*: (a) oesophageal region of ♂$_1$; (b) head of ♂$_1$; (c) head of ♂$_3$; (d) tail region of ♂$_2$; (e) copulatory apparatus of ♂$_1$; (f) spicules of three different males; (g) tails of three males and one female. Bar scales: a,d,f = 30 μm; b,c,e = 10 μm; g = 50 μm.

MATERIAL STUDIED. Holotype: ♂$_1$ BM(NH) 1981.5.38.
Allotype: ♀$_1$ BM(NH) 1981.5.39. Paratypes: four males BM(NH) 1981.5.35–37, 30.

DIMENSIONS.

Holotype ♂$_1$: $\dfrac{-\quad 83 \quad \mathrm{M} \quad 2980}{24 \quad 24 \quad 25 \quad 24}$ 3050 μm; a = 122; b = 37; c = 43; S = 38 μm

Allotype ♀$_1$: $\dfrac{-\quad 80 \quad 1900 \quad 3393}{24 \quad 25 \quad 29 \quad 21}$ 3460 μm; a = 121; b = 44; c = 52; V = 55%

♂$_2$: L = 3090 μm; a = 125; b = 51; c = 54; S = 38 μm
♂$_3$: L = 3285 μm; a = 131; b = 40; c = 54; S = 40 μm
♂$_4$: L = 2864 μm; a = 110; b = 38; c = 50; S = 37 μm
♂$_5$: L = 3155 μm; a = 131; b = 38; c = 53; S = 30 μm

(Spicule and maximum body diameter measured as in *C. macintyrei*).

DESCRIPTION. Cuticle finely striated from the base of the cephalic capsule, but most conspicuous in the oesophageal and immediate post-oesophageal regions. Typically, the cuticle is covered with a coating of coccoid blue-green algae, but this tends to be lost during preservation. The cuticle of the cephalic capsule has a feint punctated or dotted appearance viewed with interference contrast microscopy although this is difficult to depict: it is not obvious with ordinary illumination. There are rows of setae in the oesophageal region but somatic setae are absent from the rest of the body. R_1 sensilla not seen. Six small (about 1 μm) setose R_2 sensilla. Four 17–21 μm R_3 setae, about 80% of maximum cephalic capsule diameter and situated at the anterior extremity of the head. Four shorter subcephalic setae and four sublateral subamphidal setae. This disposition of the setae on the anterior part of the head was the same in all specimens. Amphid ventrally wound, situated just posterior to the R_3 setae and 6–7 μm wide. From a lateral view, the amphid appears oval but when the head is bent slightly the amphid can be seen to be round (Fig. 4c). Buccal cavity a narrow funnel in the anterior part of the buccal bulb. Tail conical with a characteristic ventral inflection in the slightly more cylindrical terminal portion.

Spicules paired, curved and proximally cephalate: average length 36 μm (arc) or 27 μm (chord). The proximal cephalation has a characteristic knob which is easy to distinguish even at low magnification (Fig. 4f). Gubernaculum well cuticularised and dorso-caudally directed. Testis single and outstretched. Tail has three pairs of subventral setae and a single precloacal ventral seta was present in at least two males.

Ovaries paired and apparently outstretched.

DIFFERENTIAL DIAGNOSIS. *Catanema smo* sp. nov. can be distinguished from most other *Catanema* species with only four subcephalic and four subamphidal setae by the anterior position of the amphid. The only other species with its amphids so far forward is *C. exile* Cobb, 1920, which has 7 well developed pairs of tubular caudal supplements.

DISCUSSION. Superficially, both the species found in the same samples from Loch Ewe appear to be similar. However, on more detailed examination they were shown to be separate species on a number of characters. In practice, the more distinct knob at the proximal end of the spicule could be used to distinguish males of *C. smo* at relatively low magnification once the existance of two separate species was realized. Other differences include the presence of two conspicuous subamphidal setae in *C. smo*, presence of somatic setae throughout the body in *C. macintyrei* and slightly smaller spicules in *C. smo*. Both species were found mainly 9–12 cm deep in the sand, the epizoic algae being a common feature on deeper-living nematodes.

Ceramonema yunfengi sp. nov.

Fig. 5(a–d)

MATERIAL STUDIED. Holotype: ♂ BM(NH) 1981.4.12.
Allotype: $♀_1$ BM(NH) 1981.4.13. Paratype $♀_2$ BM(NH) 1981.4.14.

DIMENSIONS.

Holotype ♂: $\dfrac{-\quad 181\quad \mathrm{M}\quad 1328}{16\quad 18\quad 20\quad 18}$ 1560 μm; a = 78; b = 8·6; c = 11·7; S = 24 μm

Allotype $♀_1$: $\dfrac{-\quad 125\quad \mathrm{M}\quad 791}{15\quad 17\quad 17{\cdot}5\quad 12}$ 927 μm; a = 54; b = 7·4; c = 6·8; V = 44%

$♀_2$: $\dfrac{-\quad 141\quad \mathrm{M}\quad 874}{16\quad 17{\cdot}5\quad 17{\cdot}5\quad 12{\cdot}5}$ 1020 μm; a = 58; b = 7·2; c = 7·0; V = 46%

DESCRIPTION. Body colourless, elongated and conspicuously annulated. Cuticle annules in male 5·5 μm, 7 μm and 5 μm long in the anterior oesophagus, posterior oesophagus and cloacal regions respectively. Total number of body annules 277 in ♂, 186 in $♀_1$ and 184 in $♀_2$. Each annule divided into eight plates, so that there are eight longitudinal crests running the

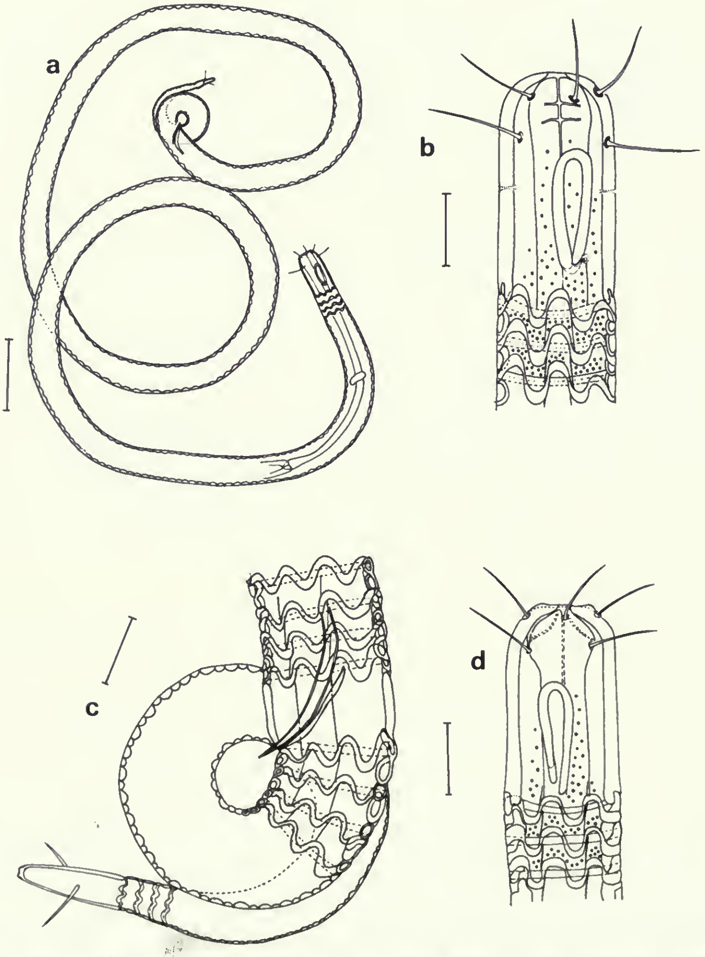

Fig. 5 *Ceramonema yunfengi*: (a) whole body of $♂_1$; (b) $♂_1$ head; (c) $♂_1$ tail; (d) $♀_1$ head. Bar scales: a = 50 μm; b–d = 10 μm.

length of the body. Vacuoles are present beneath the cuticle which are not confined to the longitudinal crests. In the male, but not the female, the annule in the cloacal region is elongated (about 12 μm) relative to the rest (Fig. 5c). Somatic setae absent except for two caudal setae situated on the distal cone of the male only. Cephalic capsule elongated: ♂ 33·5 × 16·5 μm; $♀_1$ 29 × 15 μm; $♀_2$ 31·5 × 16 μm. Six slim R_2 cephalic setae; 12·5 μm long in ♂ and 10–10·5 μm long in ♀♀. Four slim R_3 cephalic setae situated just posterior to R_2 setae; 13·5 μm long in ♂, 11 μm long in ♀♀. In the ♂, two medial holes in the cephalic capsule were observed just posterior to the level of the R_3 sensilla (Fig. 5b): possibly positions of subcuticular sensilla. Amphids an elongated loop, 17–19 μm long. Buccal cavity absent. Oesophagus narrow but widens slightly at the posterior end. Nerve ring at 52–54% of oesophagus length. Excretory ampullae situated anterior and posterior to oesophageal-intestinal junction. Tail elongated, 7 a.b.d. in ♂, 11–12 a.b.d. in ♀♀. In the ♂, the terminal cone is 14·5 μm long and bears two lateral 8 μm setae.

Spicules paired, slightly curved and 24 μm long (chord). Gubernaculum almost straight, 15 μm long. No supplements. Testes not clear.

Ovaries paired, opposed and reflexed.

DIFFERENTIAL DIAGNOSIS. *Ceramonema yunfengi* sp. nov. can be distinguished from all other known species of the genus by the presence of two lateral sub-terminal caudal setae in the ♂ and a relatively longer cephalic capsule. The only other species described which have an elongated cloacal annule are *C. carinatum* Wieser, 1959 and possibly, according to the figure, *C. pisanum* Gerlach, 1952. However, both these species have shorter cephalic setae and are not described as having subcuticular vacuolisation. In addition, the tail of *C. pisanum* is longer than that of *C. yunfengi* (11 a.b.d. vs. 7 a.b.d.).

DISCUSSION. Haspeslagh (1973) recently revised the superfamily Ceramonematoidea and, on the basis of the presence or absence of vacuolisation in the cuticle, divided *Ceramonema* into three genera. However, Lorenzen (1981) did not accept this argument and synonomized Haspeslagh's new genera, *Ceramonemoides* and *Cyttaronema*, with *Ceramonema*. Currently, there are eleven species contained in the genus including *C. yunfengi*, which can be distinguished using the data contained in Table 1 and Fig. 6.

Apart from *C. pisanum* Gerlach, 1952, which is described from a male and a juvenile female, *C. yunfengi* is the only species where both male and adult female characters are known. Four species are known from females only and one from a juvenile only. Many of the important characters used to distinguish marine nematodes in general are vested in the male, so current practice is to consider species described from females or juveniles only as dubious. However, it is still possible to separate the eleven species contained in Table 1 on the combination of the relative length of the cephalic capsule, presence or absence of vacuolisation and its pattern of distribution, relative position of R_2 and R_3 sensilla and cuticle structure. However, as more species become known, it may become impossible to separate the taxa on these characters alone so that *C. attenuatum, C. chitwoodi, C. rectum, C. sculpturatum* and *C. undulatum* may have to be designated species dubiae, particularly as certain characters display sexual dimorphism including length of R_2 and R_3 sensilla and number of body annules, at least in *C. yunfengi*. The apparent sexual dimorphism in the amphid reported for *C. pisanum* (Fig. 6e, f) may be simply due to the female not being adult: the amphids are similar in *C. yunfengi*.

Acantholaimus ewensis sp. nov.

Figs 7–8

MATERIAL STUDIED. Holotype: $♂_1$ BM(NH) 1981.4.15.
Allotype: $♀_1$ BM(NH) 1981.4.16. Paratypes: $♂_2$ BM(NH) 1981.4.17; $♂_3$ BM(NH) 1981.4.18; $♂_4$, $♂_5$ in collection of Z.N.Z.

Table I Tabular key to species of the genus *Ceramonema*

Species	sex	a	R$_3$ cephalic setae		Cephalic capsule l/w	Vacualisation +/—	Body annules	Elongated anal annule	Terminal setae	Distribution
			length	h.d.						
attenuatum Cobb, 1920	♀	?	—	0·7*	1·5*	?	?	—	?	Jamaica
carinatum Wieser, 1959	♂	43	12	0·5	1·6	—	?	+	—	E. coast USA
chitwoodi De Coninck, 1942	♀	24	9	0·3	1·1	+′	111	—	?	Mediterranean
filipjevi De Coninck, 1942	♂	33	7	0·5	1·6	—	75	—	—	Mediterranean
pisanum Gerlach, 1952	♂	67	14	0·6	1·5	?	?	+?	—	Mediterranean
rectum Gerlach, 1957	♀	23	8	0·2*	1·2*	—	?	—	?	Brazil
reticulatum Chitwood, 1936	♂	52	—	0·8*	c1·2*	+	c160	—	—	E. coast USA
salsicum Gerlach, 1956	♂	38	11	0·4	1·6	+	145	—	—	Bay of Biscay
sculpturatum Chitwood, 1936	Juv.	70	—	0·5*	c1·0*	—	?	—	?	E. coast USA
undulatum De Coninck, 1942	♀	26	4	0·3	1·5	—	78	—	?	Mediterranean
yunfengi sp. nov.	♂	78	13·5	0·8	1·9	+	277	+	+	Scotland

*calculated from figure
+′vacuoles arranged under crests only

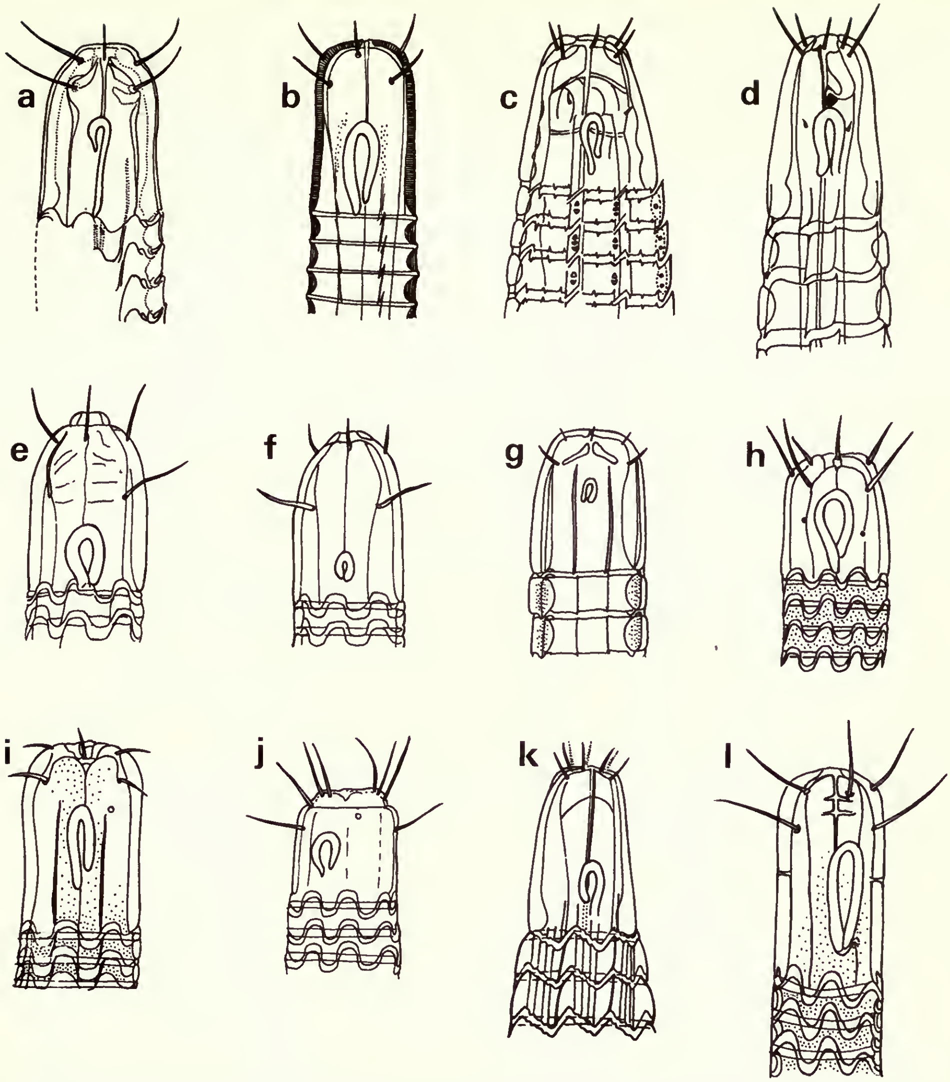

Fig. 6 Pictorial key to the species of *Ceramonema*: (a) *C. attenuatum* ♀ (after Cobb, 1920); (b) *C. carinatum* ♂ (after Wieser, 1959); (c) *C. chitwoodi* ♀ (after De Coninck, 1942); (d) *C. filipjevi* ♂ (after De Coninck, 1942); (e) *C. pisanum* ♂ (after Gerlach, 1952); (f) *C. pisanum* juvenile ♀ (after Gerlach, 1952); (g) *C. rectum* ♀ (after Gerlach, 1957); (h) *C. reticulatum* ♂ (after Chitwood, 1936); (i) *C. salsicum* ♂ (after Gerlach, 1956); (j) *C. sculpturatum* juvenile (after Chitwood, 1936); (k) *C. undulatum* ♀ (after De Coninck, 1942); (l) *C. yunfengi* sp. nov.

DIMENSIONS.

Holotype ♂$_1$: $\dfrac{-\quad 115\quad M\quad 550}{15\quad 23\quad 23\quad 19}$ 780 μm; a = 34; b = 6·8; c = 3·5; S = 28 μm

Allotype ♀$_1$: $\dfrac{-\quad 125\quad 455\quad 680}{17\quad 25\quad 32\quad 23}$ 930 μm; a = 29; b = 7·4; c = 3·7; V = 49%

♂$_2$: L = 860 μm; a = 30; b = 7·5; c = 3·7
♂$_3$: L = 875 μm; a = 35; b = 7·3; c = 3·5
♂$_4$: L = 880 μm; a = 29*; b = 7·3; c = 4·2
♂$_5$: L = 935 μm; a = 25*; b = 7·5; c = 3·5
*♂$_4$ and ♂$_5$ were slightly flattened.

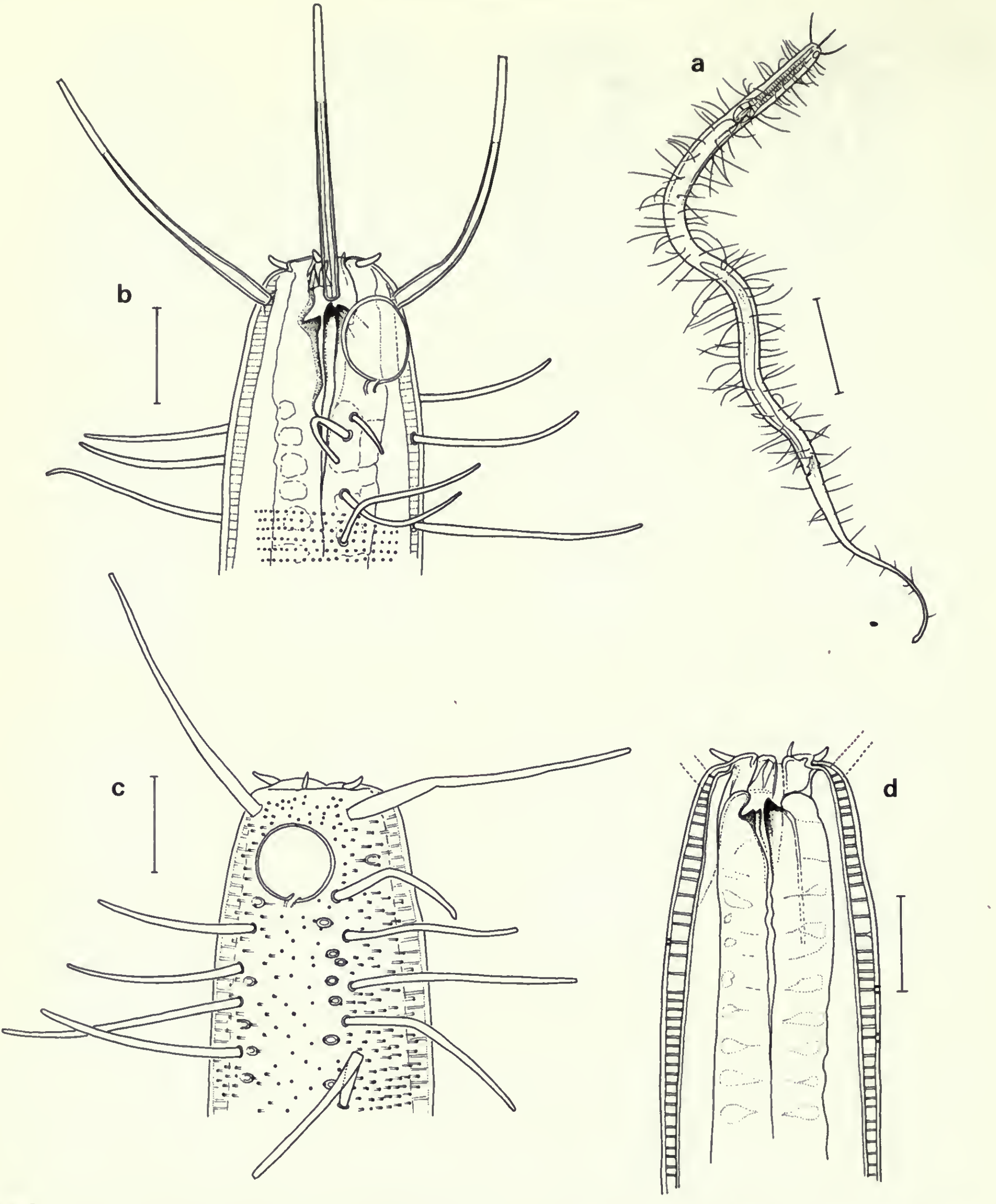

Fig. 7 *Acantholaimus ewensis*: (a) whole body of ♂$_1$; (b) head of ♂$_1$; (c) head of ♀$_1$ showing surface structures only; (d) head of ♀$_1$ showing buccal cavity structure. Bar scales: a = 100 μm; b–d = 10 μm.

DESCRIPTION. Cuticle punctated and laterally differentiated. Punctation extends anterior to amphids (Fig. 7c) and in the anterior oesophageal region the lateral punctations are irregular. Further posteriorly, the punctations become smaller and arranged in transverse rows. In the middle of the body, the transverse rows of punctations can be difficult to distinguish. Lateral differentiation consisting of two longitudinal rows of larger punctations begins level with the middle of the posterior oesophageal bulb and ends at about 65% of the tail length. The lateral rows are about 1·5 μm apart and there is a space between these rows and the transverse rows of punctations (Fig. 8f). There are four sublateral rows of hypodermal pores, which are larger anteriorly (Figs 8d–f). Long somatic setae are present throughout the length of the body and arranged more or less in four sublateral rows. In the oesophageal region, the length of the somatic setae increases from 15–20 μm at the anterior to 35–40 μm at the posterior. In the middle of the body, the longer setae are about 45 μm long but decrease in length again to about 30–40 μm in the anal region and 10–20 μm in the tail.

At the anterior extremity there is a circle of six 2·5–3 μm stout cephalic sensilla, presumably the R_2 sensilla. Just behind are four 30–33 μm R_3 cephalic setae which, in some specimens, appear to have a joint at about two-thirds of the length (Fig. 7b). Amphids 8·5–9·5 μm wide (45–50% c.d.), circular with a well cuticularised boarder and a ventrally directed posterior inflection.

Buccal cavity rather complex but basically it is conical with a distinct dorsal and two subventral teeth and anteriorly bears twelve rugae. Oesophagus has characteristic plasmatic interruptions (Fig. 7d) throughout its length and posteriorly there is a distinct bulb, 28 × 18 μm. Tail elongated (11–12 a.b.d.), gradually tapering but with a slightly bulbous tip and a pointed spinneret (Fig. 8c).

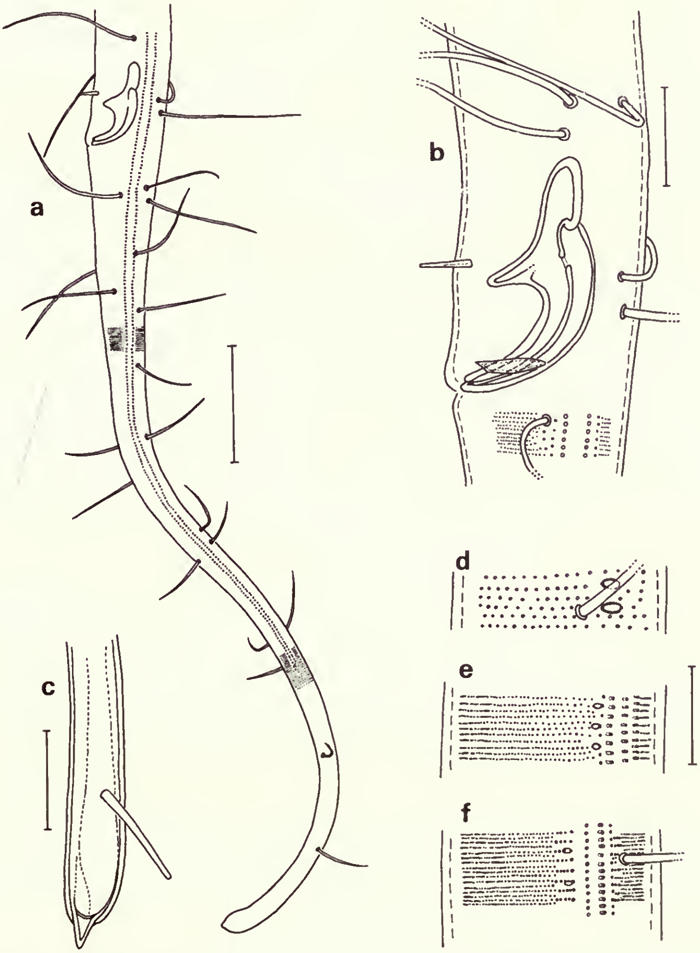

Fig. 8 *Acantholaimus ewensis*: (a) tail of ♂$_1$; (b) copulatory apparatus of ♂$_1$; (c) tail tip of ♀$_1$; (d) ♂$_1$ cuticle ornamentation about 40 μm from anterior; (e) ♂$_1$ cuticle ornamentation level with the posterior of the oesophagus; (f) ♂$_1$ cuticle ornamentation at middle of body. Bar scales: a = 30 μm; b–f = 10 μm.

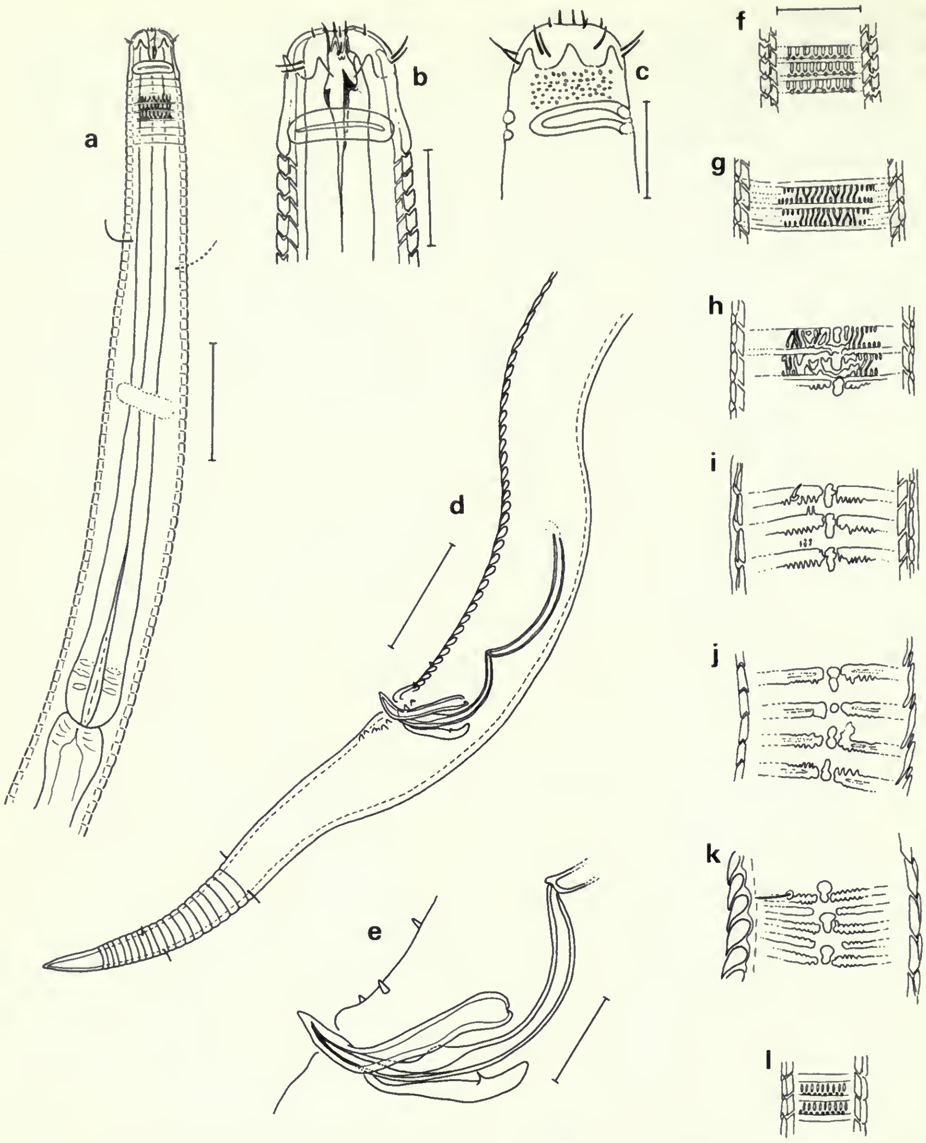

Fig. 9 *Rhips paraornata*: (a) anterior region of ♂$_1$; (b) head of ♂$_1$; (c) head of another ♂; (d) tail of ♂$_1$; (e) copulatory apparatus of ♂$_1$; (f)–(l) cuticle patterns at positions indicated in Fig. 10. Bar scales: a,d = 30 μm; b,c,e–l = 10 μm.

Spicules paired, equal, 26–28 μm long and with a characteristic ventral apophysis. Gubernaculum absent. In ♂$_1$, a feint cuticularised structure was observed lateral to the spicule (Fig. 8b): it was not detected in the other specimens. There is a single stout ventral precloacal seta, 5–6 μm long. Testis single and mature specimens contain large pear-shaped sperm.

Ovary paired, opposed and reflexed. In the female studied, there were sperm present in the oviduct and a large egg in each uterus containing a developing larva.

Differential diagnosis. *Acantholaimus ewensis* sp. nov. can be distinguished from *Acantholaimus* species with two lateral longitudinal rows of larger punctations, *A. poly-*

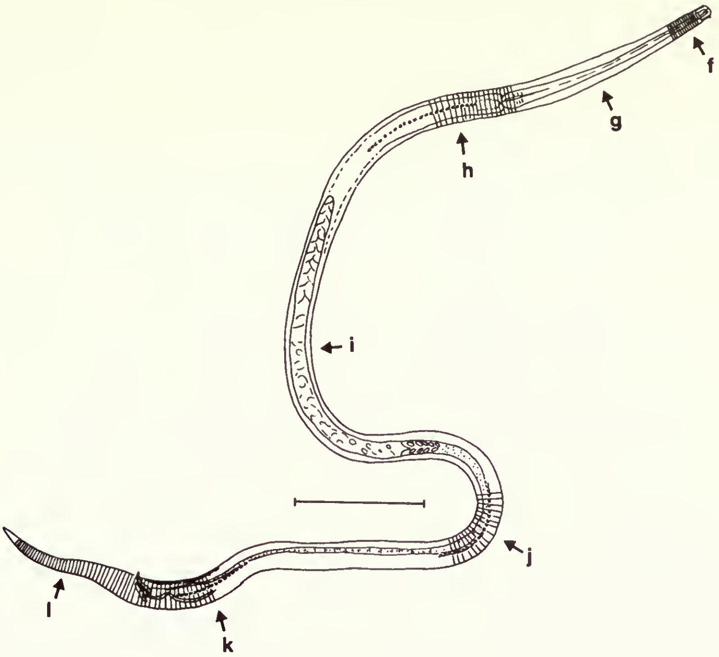

Fig. 10 *Rhips paraornata*: whole body of ♂$_1$ showing positions of cuticle pattern drawings in Fig. 9f–l. Bar scale = 100 μm.

dentatus Gerlach, 1951 and *A. calathus* Gerlach, Schrage & Riemann, 1979, on the length of the R$_3$ cephalic setae, somatic setae and tail. *A. polydentatus* has shorter cephalic setae (20–22 μm, 1·5 h.d. vs. 30–33 μm; 2·0 h.d.), shorter somatic setae (30 μm, 0·75 c.d. vs. 45 μm, 2·0 c.d.) and a shorter tail (8 a.b.d.vs. 11–12 a.b.d.). *A calathus* has shorter cephalic setae (12 μm, 1·0 h.d.), shorter setae (27 μm, 1·0 c.d.) and longer tail (17 a.b.d.).

DISCUSSION. The genus *Acantholaimus* Allgen, 1933 has been fully revised recently by Gerlach, Schrage & Riemann (1979) who described seven new forms and provided a key to the twelve known species. *A. ewensis* fits into the first part of their key as follows:

1 (4) Cuticle laterally with two longitudinal rows of larger punctations . . 2
2 (3) Amphid situated close behind the cephalic setae . . . . 2^1
2′ (2″) Tail 8 anal diameters long *A. polydentatus* Gerlach, 1951.
2″ (2′) Tail 11–12 anal diameters long *A. ewensis* sp. nov.
3 (2) Amphid situated half the head diameter behind the cephalic seta. Tail 17 anal diameters long. *A. calathus* Gerlach, Schrage & Riemann, 1979
4 (1) Cuticle with limited or no lateral differentiation, without longitudinal rows of punctations 5

Rhips paraornata sp. nov.

Figs 9–10

MATERIAL STUDIED. Holotype: ♂$_1$ BM(NH) 1981.4.19.
Allotype: ♀$_1$ BM(NH) 1981.4.20. Paratypes: nine males and two females; ♂$_6$ BM(NH) 1981.4.21, remainder in collection of Z.N.Z.

DIMENSIONS.

Holotype ♂$_1$: $\dfrac{-\ \ 180\ \ M\ \ 990}{11\ \ \ 21\ \ 23\ \ \ 22}$ 1105 µm; a = 48; b = 6·1; c = 9·6; S = 78 µm

Allotype ♀$_1$: $\dfrac{-\ \ 179\ \ M\ \ 938}{10\ \ \ 26\ \ 29\ \ \ 20}$ 1080 µm; a = 37; b = 6·0; c = 7·6; V = 54%

♂$_2$: L = 1085 µm; a = 38; b = 6·1; c = 8·7
♂$_3$: L = 1330 µm; a = 50; b = 6·5; c = 9·3
♂$_4$: L = 1130 µm; a = 48; b = 6·5; c = 11·9
♂$_5$: L = 1260 µm; a = 44; b = 6·4; c = 8·5
♂$_6$: L = 1260 µm; a = 47; b = 6·9; c = 11·0
♂$_7$: L = 920 µm; a = 42; b = 5·3; c = 8·7
♂$_8$: L = 1280 µm; a = 53; b = 6·7; c = 10·0
♂$_9$: L = 1275 µm; a = 53; b = 7·4; c = 13·0
♂$_{10}$: L = 1160 µm; a = 50; b = 6·9; c = 9·0
♀$_2$: L = 1095 µm; a = 44; b = 6·6; c = 9·0
♀$_3$: L = 980 µm; a = 36; b = 6·5; c = 7·3

DESCRIPTION. The cuticle is conspicuously annulated and heterogeneously ornamented laterally. In the anterior third of the oesophagus, from about the point where the body characteristically narrows (Fig. 9a) each annule bears a row of long and a row of smaller round punctations (Fig. 9f), the latter being difficult to distinguish and liable to be overlooked. In the posterior part of the oesophagus, the punctations are smaller and appear to be partly linked diagonally (Fig. 9g), giving a reticulated appearance. The regular nature of the ornamentation breaks down posterior to the oesophagus and lateral differentiation of large dumb-bell-shaped punctations begins (Fig. 9h). Just posterior to the mid-point of the body, the pattern of the lateral differentiation reverses and, at the point of change, the dumb-bell-shaped lateral punctation is represented by a single round dot (Fig. 9j). Lateral differentiation ends just anterior to the anus and transverse rows of discrete punctations are present on the tail (Fig. 9l).

Short 4–6 µm sublateral somatic setae are present at infrequent intervals throughout the body and at a third of the oesophagus length, there are four longer somatic setae (Fig. 9a). The head bears six setose R_1 sensilla. The six 2–3 µm R_2 sensilla are situated just anterior to the four shorter (1·5–2 µm), R_3 sensilla. The elongated first body annule forms a cephalic shield and bears six triangular flap-like extensions anteriorly which alternate with the $R_2 + R_3$ sensilla (Fig. 9b, c). The shield is irregularly punctated and bears the large transverse amphids. The amphid has strongly cuticularised borders and is 11 µm wide, about 0·85 c.b.d. The buccal cavity is surrounded anteriorly by rugae which protrude beyond the lips. There is a large pointed dorsal tooth and two smaller subventral teeth. The oesophagus widens posteriorly to a weak bulb. The tail is conical and has an unstriated end cone.

The male copulatory apparatus is complex, consisting of two long double-jointed spicules, a paired gubernaculum and two lateral pieces. In the holotype, the posterior part of the spicule measures 40 µm as the arc (or 29 µm as the chord) and the anterior part measures 38 µm as the arc (or 35 µm as the chord). In five other males, the total arc length of the spicule is 70–96 µm. The lateral pieces are about 22 µm long and the gubernaculum 18 µm. The cloacal opening is surrounded by irregular cuticular excrescences and anteriorly there is a small ventral spine. The ventral part of the precloacal body rings are more thickly cuticularised: they gradually reduce in thickness anterior to the level of the proximal end of the spicules (Fig. 9d). There is a single testis situated to the right of the gut. The female has two opposed, reflexed ovaries.

DIFFERENTIAL DIAGNOSIS. *Rhips paraornata* sp. nov. can be distinguished from the only other valid species in the genus, *R. ornata* Cobb, 1920, by having slightly shorter R_2 cephalic setae, wider amphids, spicules with each part about the same length and possibly a differently shaped lateral differentiation.

DISCUSSION. This is only the fifth time that valid specimens of this genus have been reported. Timm (1961) described a species *R. longicauda* from the Bay of Bengal, but the description is very poor and based only on a single immature female: it must be considered a dubious species.

The original description of the type and only other species, *R. ornata*, was by Cobb (1920): the specimens from Loch Ewe are clearly similar to this species from Florida. The species was found again by Wieser & Hopper (1967) who provide a brief redescription and figure the head. Allgen (1932) found what is certainly a male *Rhips* species from Campbell Island and considered it conspecific with Cobb's species and Gerlach (1957) found *R. ornata* in Brazil but did not describe it.

Cobb (1920) described the unusual triangular scale-like cephalic flaps but only saw the four sublateral ones: Wieser & Hopper (1967) correctly observed all six. The four long cervical setae, located at about one-third the oesophagus length in *R. paraornata*, were not reported in *R. ornata* but they are fine and may be lost on handling so that their absence in *R. ornata* cannot be assumed. The four sublateral cephalic flaps were positioned 'just in front of the ends of the amphids' in *R. ornata* according to Cobb (1920) and as figured by Wieser & Hopper (1967), whilst the ends of the amphids in *R. paraornata* extend further beyond the flaps. Both Cobb (1920) and Wieser & Hopper (1967) describe the lateral differentiation in the posterior portion of the body as being 'V'-shaped but unfortunately provide no illustrations of the cuticle patterns. If the lateral differentiation is similar in both species, then we would not have chosen to describe the lateral differentiation as 'V'-shaped. It is possible, then, that the cuticle patterns are different. Finally, the spicules of *R. ornata* have an anterior part which is 1·5 times the length of the posterior part whilst in *R. paraornata* the lengths are almost the same, measured as the arc in both cases. Therefore, although there are many points of similarity in overall dimensions and general anatomy, there are sufficient points of difference in relation to the specific sizes of cephalic setae, amphids and spicules and possibly the form of the cuticle lateral differentiation to substantiate the creation of a new species for the specimens from Loch Ewe.

Species of the genus *Rhips* seem to be very closely related to *Actinonema,* particularly through the excellent redescription of the common species *A. pachydermatum* Cobb, 1920 by Lorenzen (1972): both have similar amphids, cuticle patterns and the six triangular extensions to the cephalic shield, 'Kopfpanzer', although the flaps in *A. pachydermatum* are not as conspicuous as those in *R. paraornatum* and may have been overlooked by earlier workers. However, *Actinonema* does not have large double-jointed spicules and, according to Lorenzen (1972), between those structures which he terms spicules, but which resemble the lateral pieces of *Rhips,* there lies a single thin cuticularised tube which Lorenzen (1972) interprets as the cuticularised terminal portion of the vas deferens. We have studied several specimens of *A. pachydermatum*, sympatric with *R. paraornata*, and find the cuticularised tube very difficult to distinguish. However, in some specimens it is just possible to make out two tubes: if so, they cannot be vas deferens since *A. pachydermatum* is monorchic. This problem is of systematic importance since *Rhips* and *Actinomena*, together with a number of other genera including *Euchromadora,* are grouped together in the subfamily Euchromadorinae. This subfamily was erected by Gerlach & Riemann (1973) without explanation but presumably because of the presence of the 'L'-shaped lateral pieces in addition to spicules and gubernaculum. For *Actinonema* to fit into this group, which seems reasonable through its similarity to *Rhips*, the spicules of *Actinonema* must be considered homologous with the lateral pieces of *Rhips* and either the cuticularised tube(s?) are vestigial spicules or spicules are absent. For the moment, this problem must remain open for further study.

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The larval development of *Crangon crangon* (Fabr. 1795) (Crustacea: Decapoda)

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Introduction

The first larval stage of *Crangon crangon* (Fabr., 1795) was recorded by Du Cane in 1839 and since then descriptions of some of the subsequent larval stages have been added. In 1890 Ehrenbaum described five larval stages but suggested, as they were taken from plankton samples, that his series may not have been complete. Williamson (1901) reared the first three stages in the laboratory, and selected examples from tow net plankton samples concluding that there were probably five larval stages in all. Experimental evidence on the development of larvae under non-circadian light/dark cycles given by Dalley (1980), also suggested there were five larval stages. The present study is based on specimens reared in the laboratory, and describes six larval stages, one more than those previously recorded.

Materials and method

Ovigerous *Crangon crangon* (Fabr., 1795) were trawled in the Sound, Plymouth, in March, 1980. Rearing techniques follow those of Fincham, 1977. Representatives of each stage are deposited in the Crustacea collections of the British Museum (Natural History), registration numbers 1981 : 394–400.

Description of larval stages

Key characters are printed in *italic type*; many setal counts have been omitted but these are recorded in Table 1.

ZOEA 1 (Fig. 1) mean size 2 mm
Head (Figs 1a, b): eyes are sessile.
Carapace (Figs 1a, b): without spines; rostrum short.
Antenna 1 (Fig. 1c): *single peduncle segment* bearing external flagellar segment with *three aesthetascs* distally plus one seta; terminal setose spine on peduncle segment.
Antenna 2 (Fig. 1d): expodite broad and flat with *ten setae, all plumose except the penultimate, subapical medial spine absent*; endopodite with terminal spinous seta; spine on distal edge of peduncle segment at base of endopodite.
Mandibles (Fig. 1e): symmetrical.
Maxilla 1 (Fig. 1f): coxa with seven spines; basis with five spines; endopod with five setae plus one small spine.
Maxilla 2 (Figs 1g, h): endopod coxa bilobed on inner margin, *proximal lobe with six setae*, distal lobe with four setae; basis one with four setae; basis two with four setae, endopodite with four lobes on inner margin, fourth proximal lobe with three setae, third sub proximal lobe with two setae, second subdistal lobe with one seta, distal lobe with two setae; *exopodite with five setae*.

Maxillipeds 1–3 (Figs 1i–l): with natatory exopodites.
Pereiopod 1 (Fig. 1m): *rudimentary, biramous.*
Pereiopods 2–4 (Figs 1m): rudimentary, uniramous.
Pereiopod 5: absent.
Abdomen (figs 1a, b): 5 somites, *6th somite continuous with telson.*
Telson (Fig. 1n): fans out distally, *distal margin with 7 + 7 terminal plumose spines.*

Zoea 2 (Fig. 2) mean size 2·4 mm
Head (Figs 2a, b): eyes 'stalked'.
Antenna 1 (Fig. 2c): peduncle two segmented; internal distal margin of second segment extended.
Pereiopod 1 (Fig. 2m): *1-segmented endopod with one apical seta; natatory exopodite.*
Telson (Fig. 2o): *distal margin with 8 + 8 terminal plumose spines.*

Zoea 3 (Fig. 3) mean size 3·0 mm
Antenna 1 (Fig. 3c): *external flagellum with four distal aesthetascs, one narrower than others* and one distal seta.
Pereiopod 1 (Fig. 3k): 2-segmented endopodite.
Telson (Fig. 3n): *divided from somite 6 by suture; exopod and endopod of uropod with fringing plumose setae.*

Zoea 4 (Figs 4 & 5) mean size 3·5 mm
Antenna 1 (Fig. 4c): rudimentary stylocerite.
Periopod 1 (Fig. 5d): *3-segmented endopodite.*
Abdomen (Fig. 4b): rudimentary buds of pleopods on somites 1–5.

Zoea 5 (Figs 6 & 7) mean size 4·1 mm
Antenna 1 (Fig. 6c): *external flagellum segment with 4 wide distal aesthetascs and one narrow sub-distal aesthetasc* plus one setule.
Pereiopod 1 (Fig. 7d): *4-segmented endopodite.*
Pereiopods 2–3 (Fig. 7e): uniramous 1-segmented.
Pereiopod 4 (Fig. 7f): uniramous *4-segmented.*
Pereiopod 5 (Fig. 7g): uniramous *5-segmented.*

Zoea 6 (Figs 8 & 9) mean size 4·2 mm
Pereiopod 1 (Fig. 9d): *5-segmented endopodite.*
Pereiopods 2–5 (Figs 9e–f): *uniramous 6-segmented.*

Post larva 1 (Figs 10–12) mean size 4·4 mm
Carapace (Figs 10a, b): rostrum short; one dorso-medial tooth.
Antenna 1 (Fig. 10c): 3-segmented peduncle; external flagellum 2-segmented with four distal and two sub-distal aesthetascs, internal flagellum 3-segmented; stylocerite with terminal plumose setae.
Antenna 2 (Fig. 10d): exopodite with 19 plumose setae; *endopodite multisegmented.*
Mandibles (Fig. 10e): symmetrical.
Maxilla 1 (Fig. 10f): coxa with 5 spines; basis with 9 spines plus one plumose seta; endopod with one spine.
Maxilla 2 (Fig. 10g): endopod reduced; exopod >22 plumose setae.
Maxilliped 1 (Fig. 11a): endopod reduced with one plumose seta; exopod with 3 short plumose setae distally plus one seta, one plumose seta proximally; epipodite present.
Maxilliped 2 (Figs. 11b, c): endopod 5-segmented, exopod with reduced setae.
Maxilliped 3 (Fig. 11d): endopod 3-segmented; exopod with very reduced plumose setae.
Pereiopod 1 (Figs 11e, f): *exopod reduced*; endopod 4-segmented, *propodus and dactylus subchelate.*
Pereiopod 2 (Fig. 11g): 5-segmented, chelate; epipodite present.
Pereiopod 3 (Figs 11h, i): 7-segmented.

Table 1 Morphological comparison of larval stages 1–6 and post larva. (v = visible; d = developed; a = absent; p = present; r = rudimentary; b = biramous; re = reduced)

ZOEA STAGE	1	2	3	4	5	6	PL
MEAN SIZE	2·0 mm	2·4 mm	3·0 mm	3·5 mm	4·1 mm	4·2 mm	4·4 mm
ANTENNA 1							
No. of aesthetascs.	3	3	4	4	5	6	6
Stylocerite.	a	a	a	v	v	v	d
No. of segments.	**1**	2	2	2	2	2	3
ANTENNA 2							
Presence of subapical medial spine.	**a**	p	p	p	p	p	p
Exopodite; no. of plumose setae incl. fine setae immediately after spine.	10	11	12–13	13–14	13–14	14–16	19
MAXILLA 1							
No. of setae on coxa;	7	7	7	7	8	8	1
basis;	**5**	7	8	8	9	9	10
endopod.	5 + 1	5 + 1	5 + 1	5 + 1	5 + 1	5 + 1	4 + 1
MAXILLA 2							
No. of endite setae on endopodite lobes 1, 2, 3, 4;	2.1.2.3	2.1.2.3	2.1.2.3	2.1.2.3	2.1.2.3	2.1.2.3	re
basis 1;	4	4	4	4	4	4	re
basis 2;	4	4	4	4	4	4	re
coxa (prox. & distal).	**6 + 4**	7 + 4	7 + 4	7 + 4	7 + 4	7 + 4	re
No. of plumose setae on exopodite.	**5**	**10**	10–13	13–15	15–19	20–22	> 22
MAXILLIPED 1							
No. of setae on endite of coxa;	**4**	**5**	5	5	5	5	re
basis.	**11**	**13**	14	14	14	14	re
No. of plumose setae on exopodite.	**4**	**5**	5	5	5	5	re
PEREIOPOD 1							
No. of segments in endopodite.	**r/b**	**1**	**2**	**3**	**4**	**5**	4
No. of setae on endopodite.	**a**	**1**	**2**	v	v	v	–
Presence of natatory exopodite.	**a**	**p**	p	p	p	p	re
PEREIOPOD 2							
No. of segments.	r	r	r	r	r	**6**	5
No. of setae.	–	–	–	–	1	1	–
PEREIOPOD 3							
No. of segments.	r	r	r	r	r	**6**	**7**
No. of setae.	–	–	–	–	1	1	–
PEREIOPOD 4							
No. of segments.	r	r	r	r	**4**	**6**	**7**
PEREIOPOD 5							
No. of segments.	a	r	r	r	**5**	**6**	**7**
ABDOMEN							
Somite 6—distal suture present.	**a**	a	p	p	p	p	p
TELSON							
No. of segments.	**14**	16	16	16	16	16	**10**
UROPODS							
Presence.	a	a	p	p	p	p	p

Pereiopod 4 (Figs 11j, k): 7-segmented.
Pereiopod 5 (Figs 11l, m): 7-segmented.
Pleopod 1 (Fig. 12a): inner margin of exopod with 6 plumose setae, 2 apical setae, external margin with 4 plumose setae.
Pleopods 2–4 (Figs 12b–d): exopod inner margin 6 plumose setae, 2 apical setae, external margin with 5 plumose setae.
Pleopod 5 (Fig. 12e): exopod inner margin with 5 plumose setae, 2 apical setae, external margin with 4 plumose setae.
Telson (Fig. 12f): *5 + 5 spines*; exopod of uropod with one spine next to subapical medial spine.

Discussion

The larval stages of *Crangon crangon* (Fabr., 1795) have not previously been described solely from laboratory reared material. Williamson (1901) figured his larval series from the first three stages reared in the laboratory, supplemented by larval stages four and five and the post larva taken from plankton samples. All earlier records indicate five larval stages. In the present work six larval stages are produced consistently under laboratory conditions. The insertion of an additional larval stage prolonging development is a feature shared by other carideans (Fincham, 1977). In planktonic larvae delaying the onset of metamorphosis until conditions are favourable provides the maximum chance of survival for the mainly benthic juveniles.

Minor differences related to the insertion of an additional larval stage become apparent when comparisons to Williamson's (1901) work are made. The numbers of aesthetascs recorded in this paper accord with Williamson up to stage four when he then records 6 (4 distal and 2 subdistal) compared with 5 aesthetascs (4 distal and 1 subdistal) for stage 5; 7 (4 distal and 3 subdistal) in first post larva compared with 6 (4 distal and 2 subdistal) in post larva recorded here. Maxilliped 1 showed variation in the early stages. Williamson records 10 spines on the basis in stage 1, 12 in stage 2, 13 in stage 3 compared with 11 in stage 1, 13 in stage 2 and 14 in stage 3 recorded here. Pereiopods 2–5 in the last two larval stages differed in segmentation. Williamson showed stage 4 pereiopod 2 as 1-segmented, pereiopod 3 as 3-segmented and pereiopods 4 and 5 as 2-segmented; stage 5 pereiopods 2–5 as 7-segmented. Recorded in this paper stage 5 pereiopod 2 is rudimentary, pereiopod 3 is 1-segmented, pereiopod 4 is 4-segmented and pereiopod 5 is 5-segmented; stage 6 pereiopods 2–5 are 6-segmented. These differences are almost certainly related to the insertion of the extra larval stage after stage 2 prior to metamorphosis.

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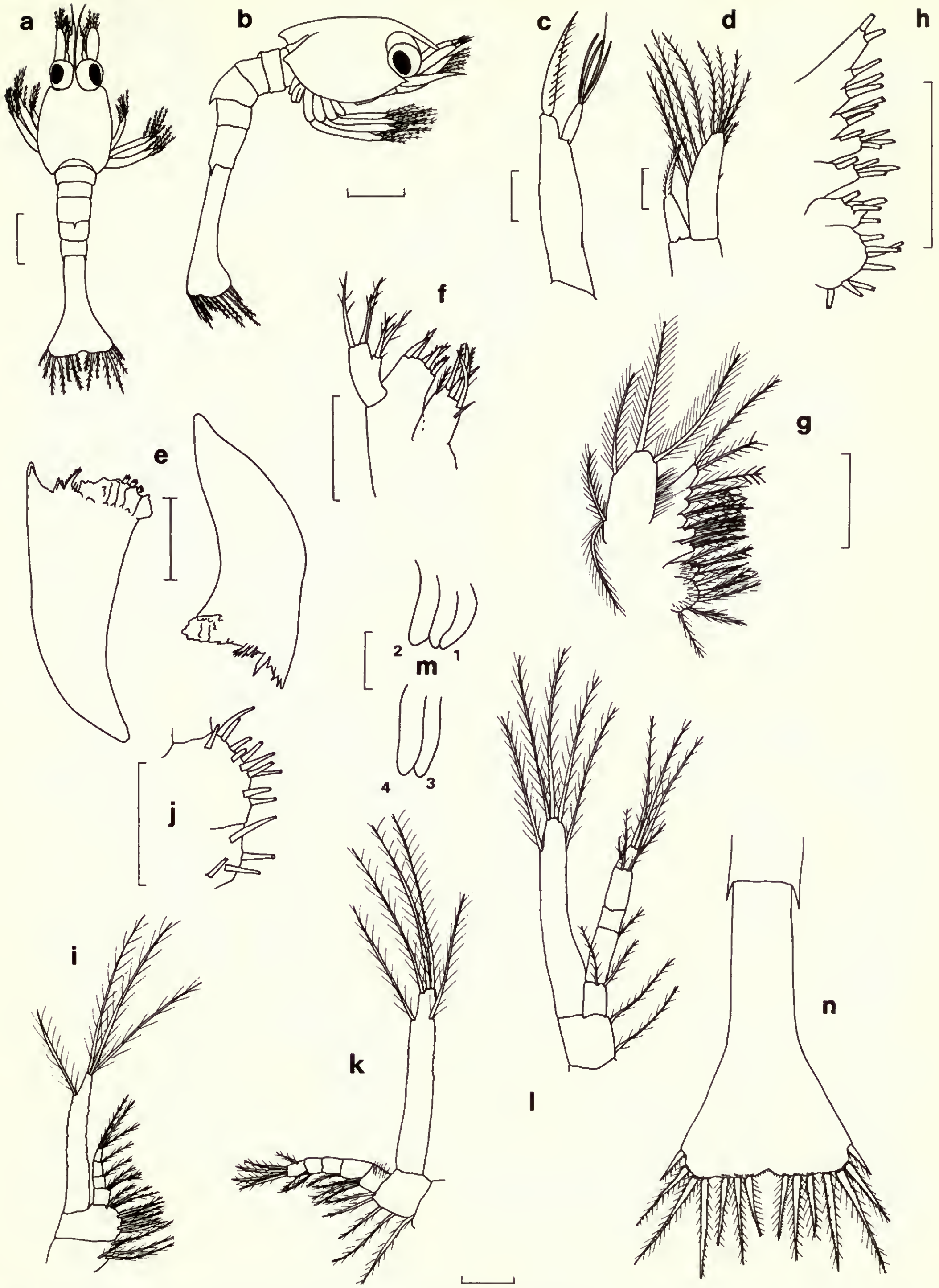

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) armature of maxilla 2; (i) maxilliped 1; (j) armature of maxilliped 1; (k) maxilliped 2; (l) maxilliped 3; (m) pereiopods 1–5; (n) telson.
Bar scales: a, b = 0·35 mm; c–n = 0·1 mm.

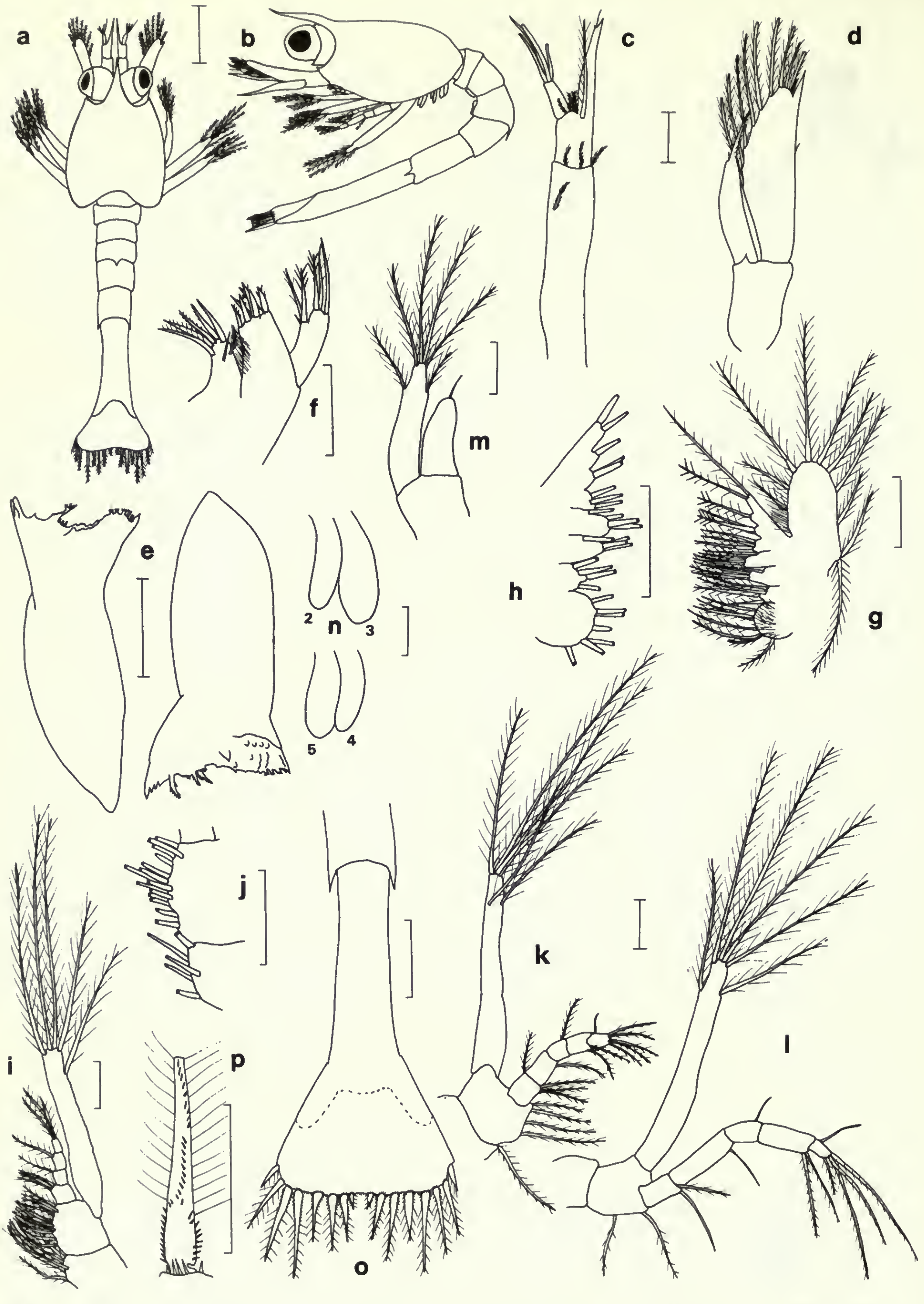

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) armature of maxilla 2; (i) maxilliped 1; (j) armature of maxilliped 1; (k) maxilliped 2; (l) maxilliped 3; (m) pereiopod 1; (n) pereiopods 2–5; (o) telson; (p) detail of spine, 3rd from right, on telson.
Bar scales: a, b = 0·3 mm; c–p = 0·1 mm.

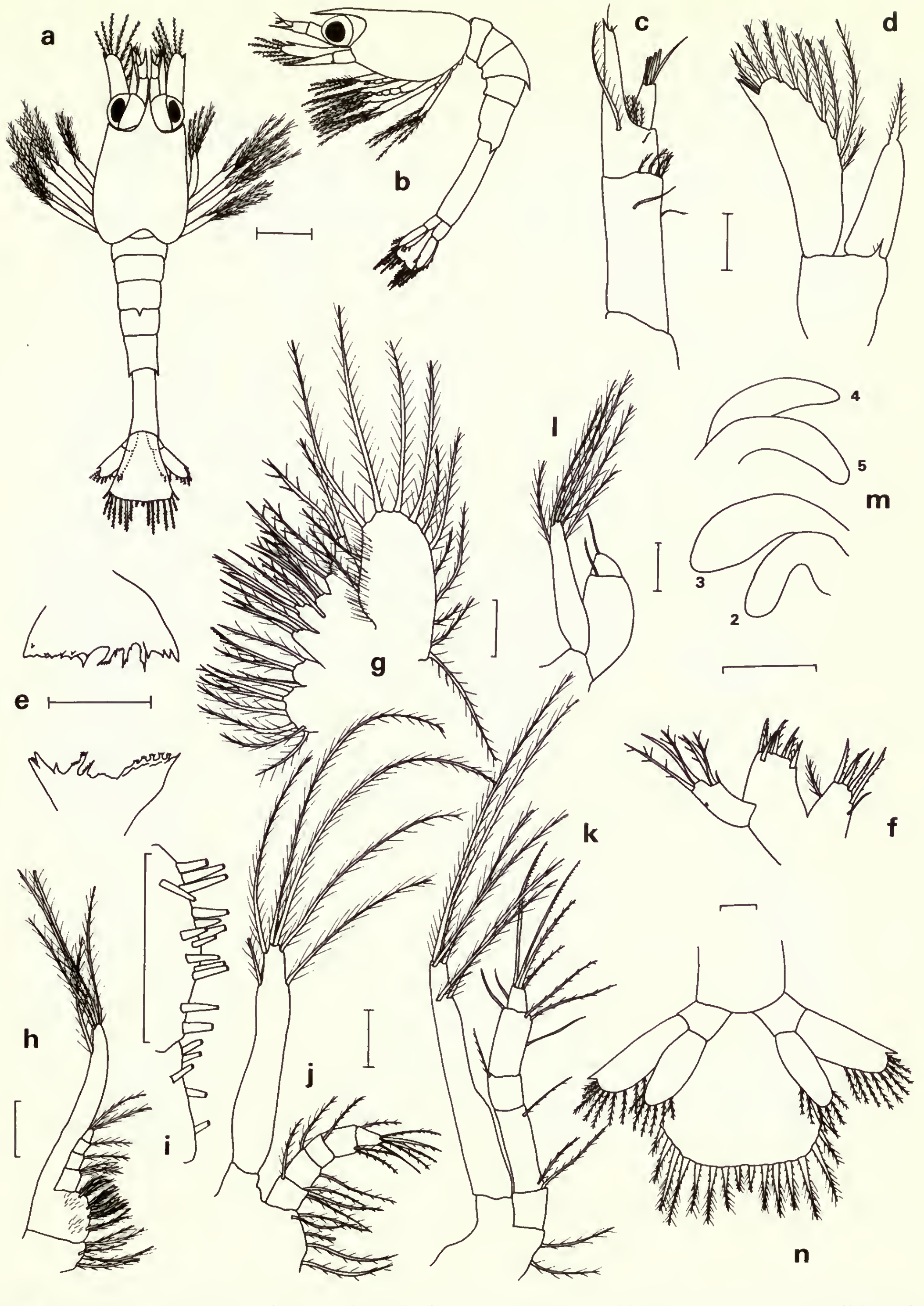

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) armature of maxilliped 1; (j) maxilliped 2; (k) maxilliped 3; (l) pereiopod 1; (m) pereiopods 2–5; (n) telson.
Bar scales: a, b = 0·2 mm; c–g = 0·1 mm.

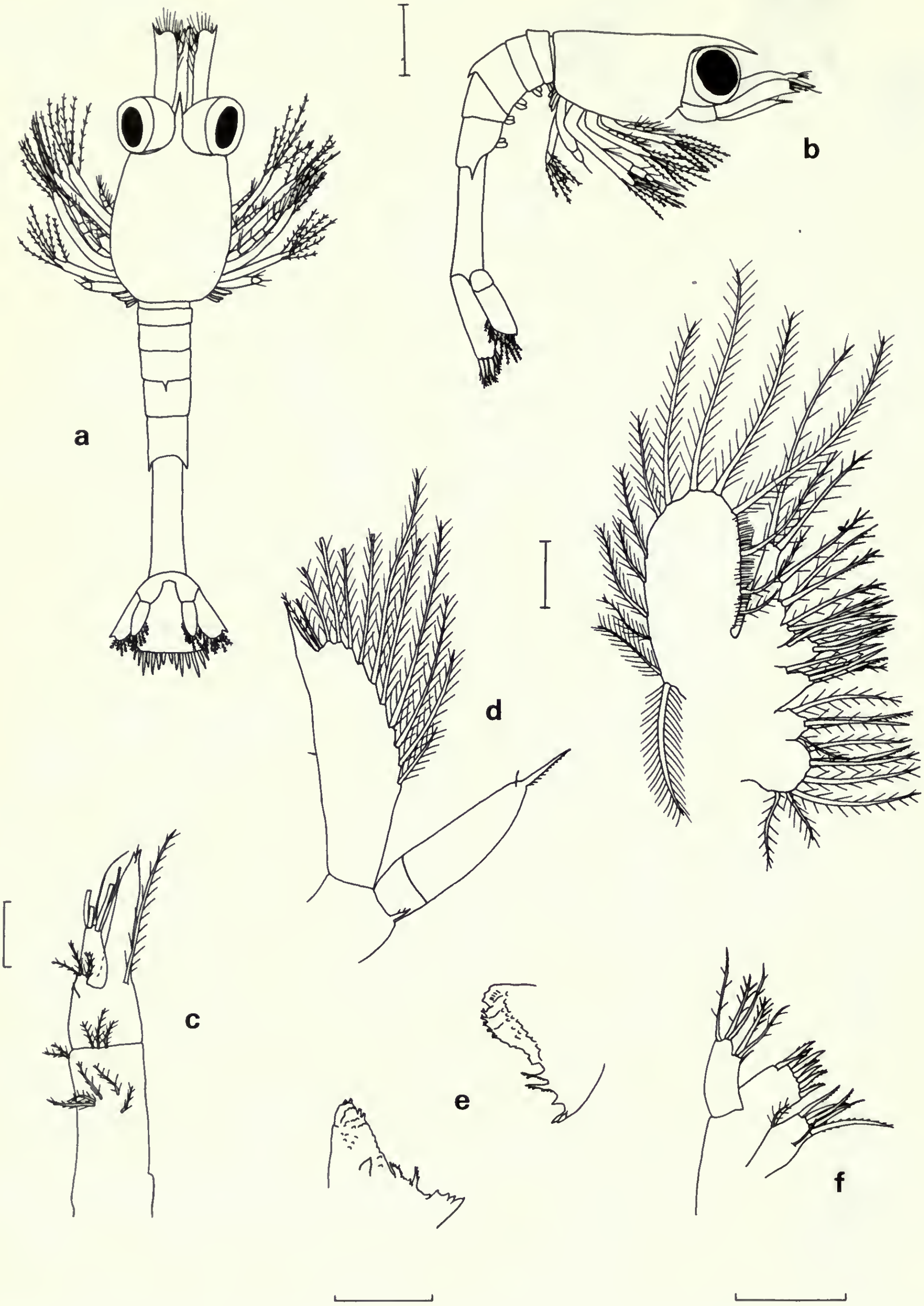

Fig. 4 Zoea 4: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2.
Bar scales: a, b = 0·3 mm; c–g = 0·1 mm.

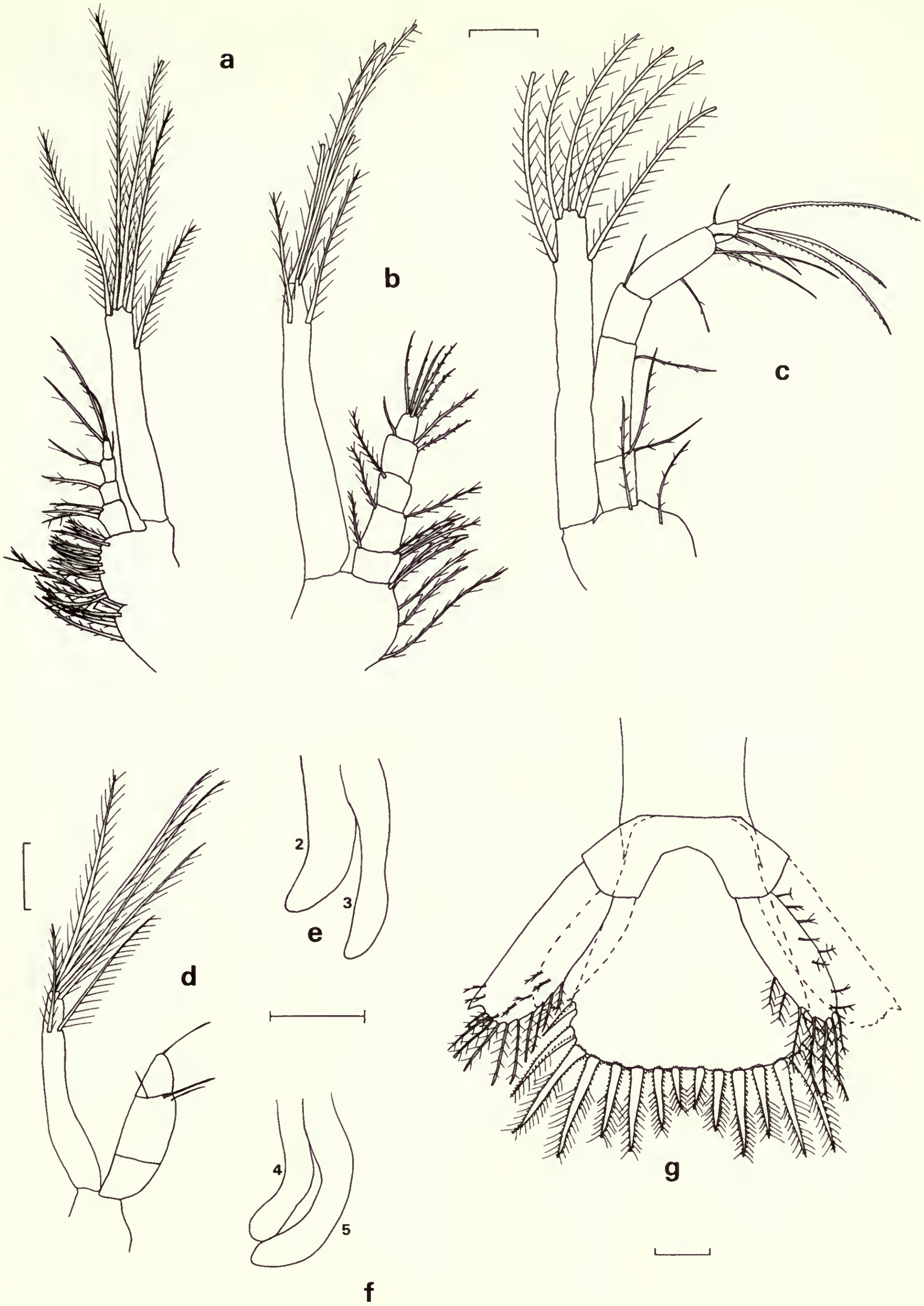

Fig. 5 Zoea 4: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopods 2 & 3; (f) pereiopods 4 & 5; (g) telson.
Bar scales: a–g = 0·1 mm.

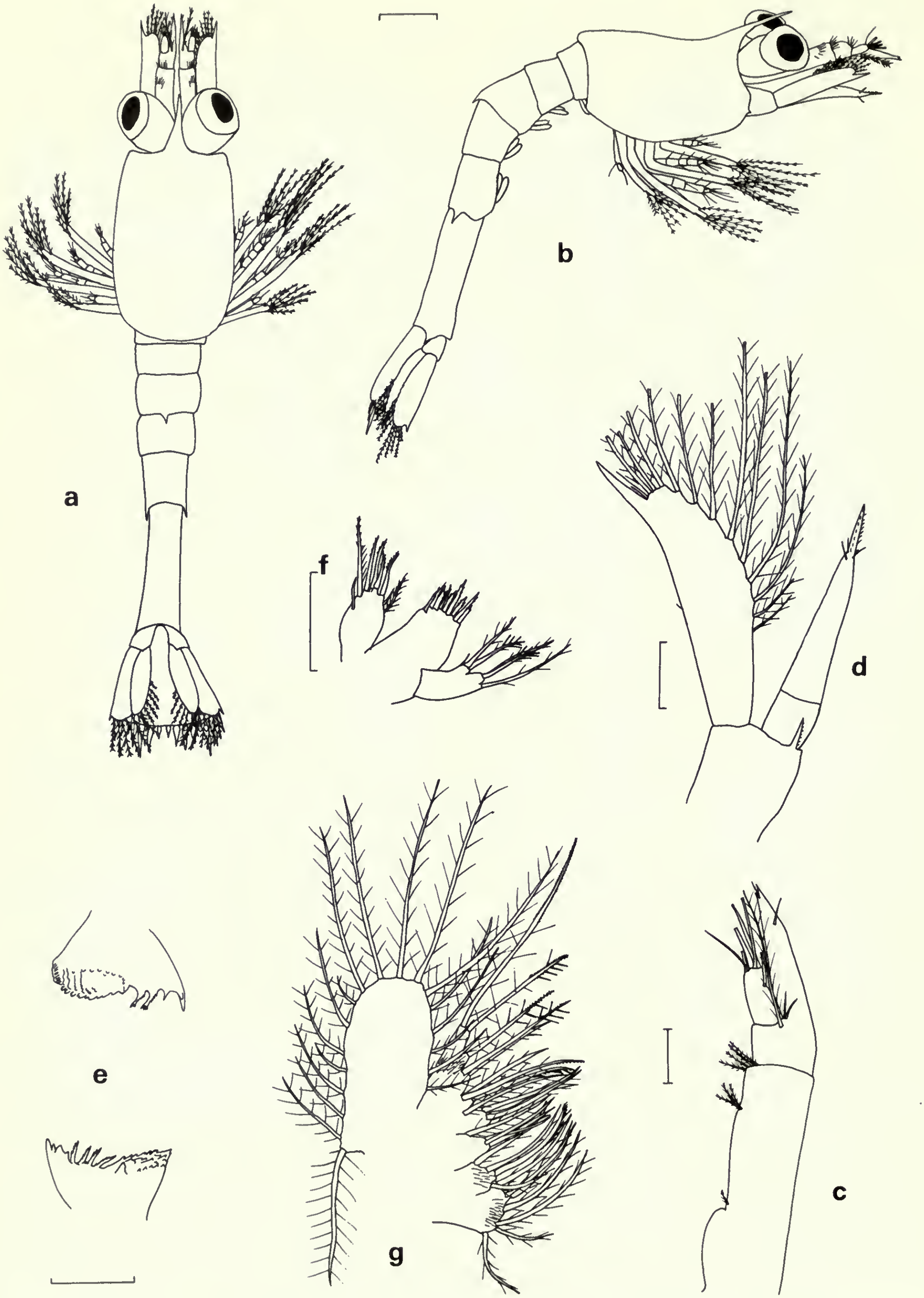

Fig. 6 Zoea 5: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2.
Bar scales: a, b = 0·3 mm; c–g = 0·1 mm.

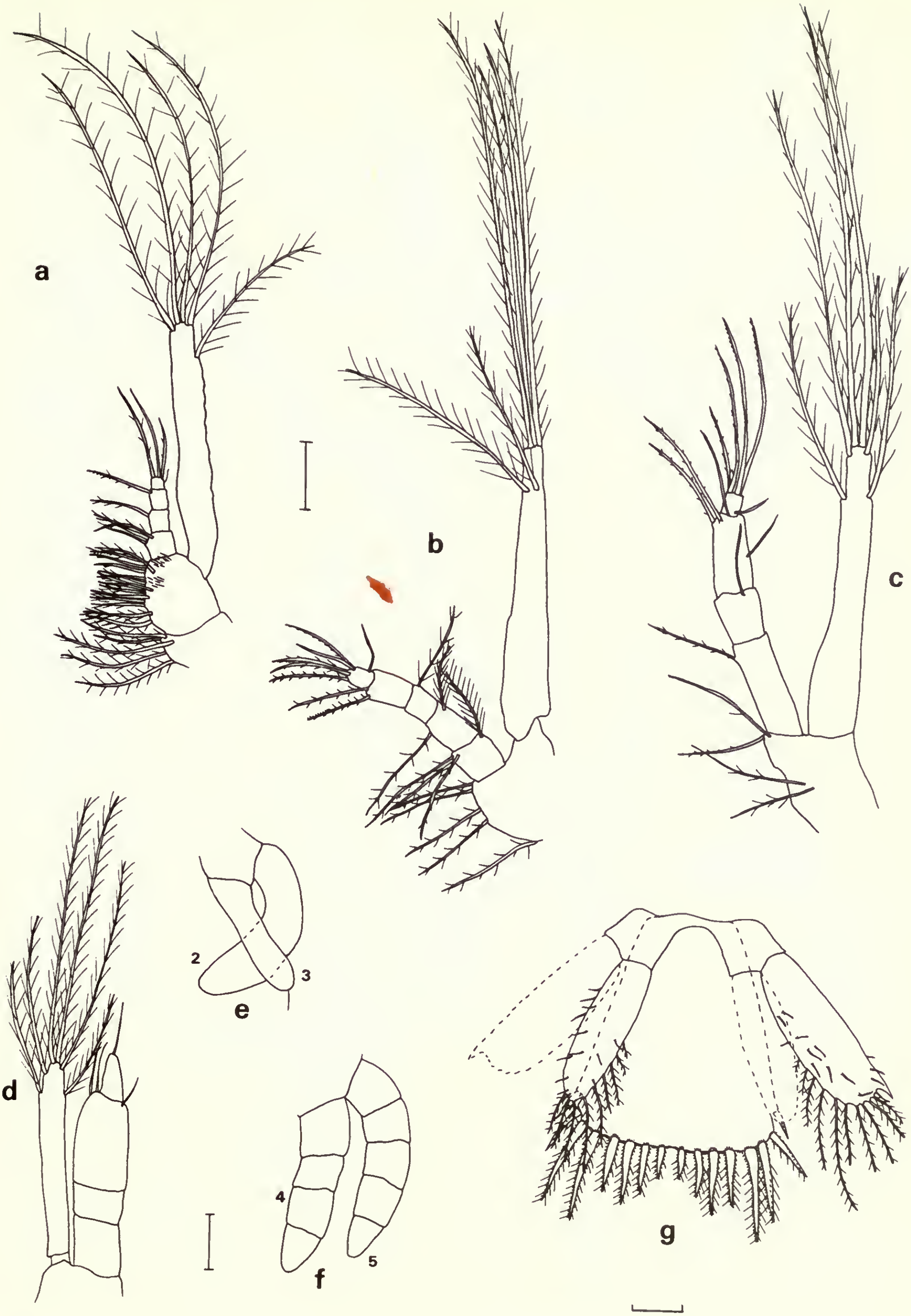

Fig. 7 Zoea 5: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopods 2 & 3; (f) pereiopods 4 & 5; (g) telson.
Bar scales: a–g = 0·1 mm.

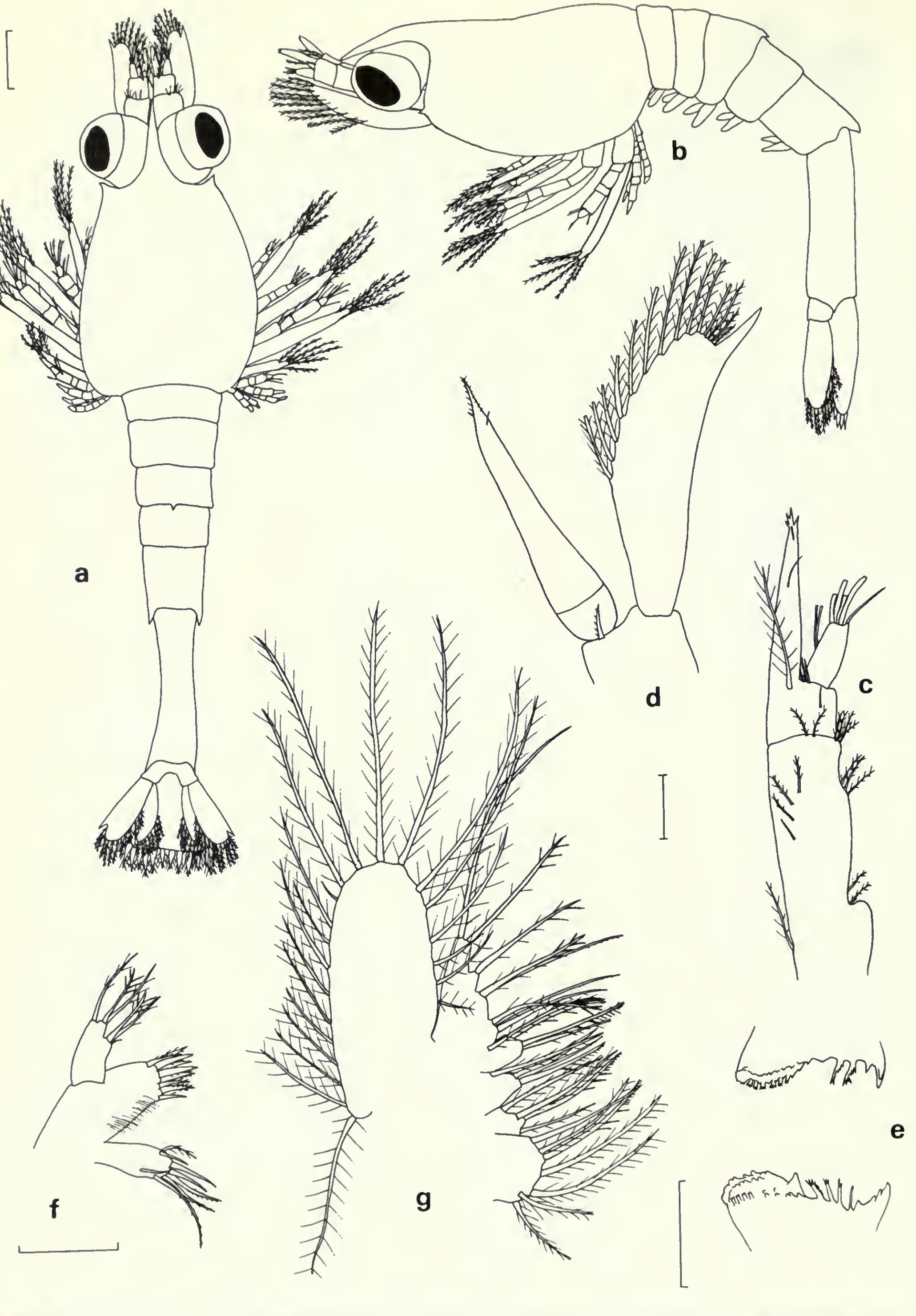

Fig. 8 Zoea 6: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2.
Bar scales: a, b = 0·3 mm; c–g = 0·1 mm.

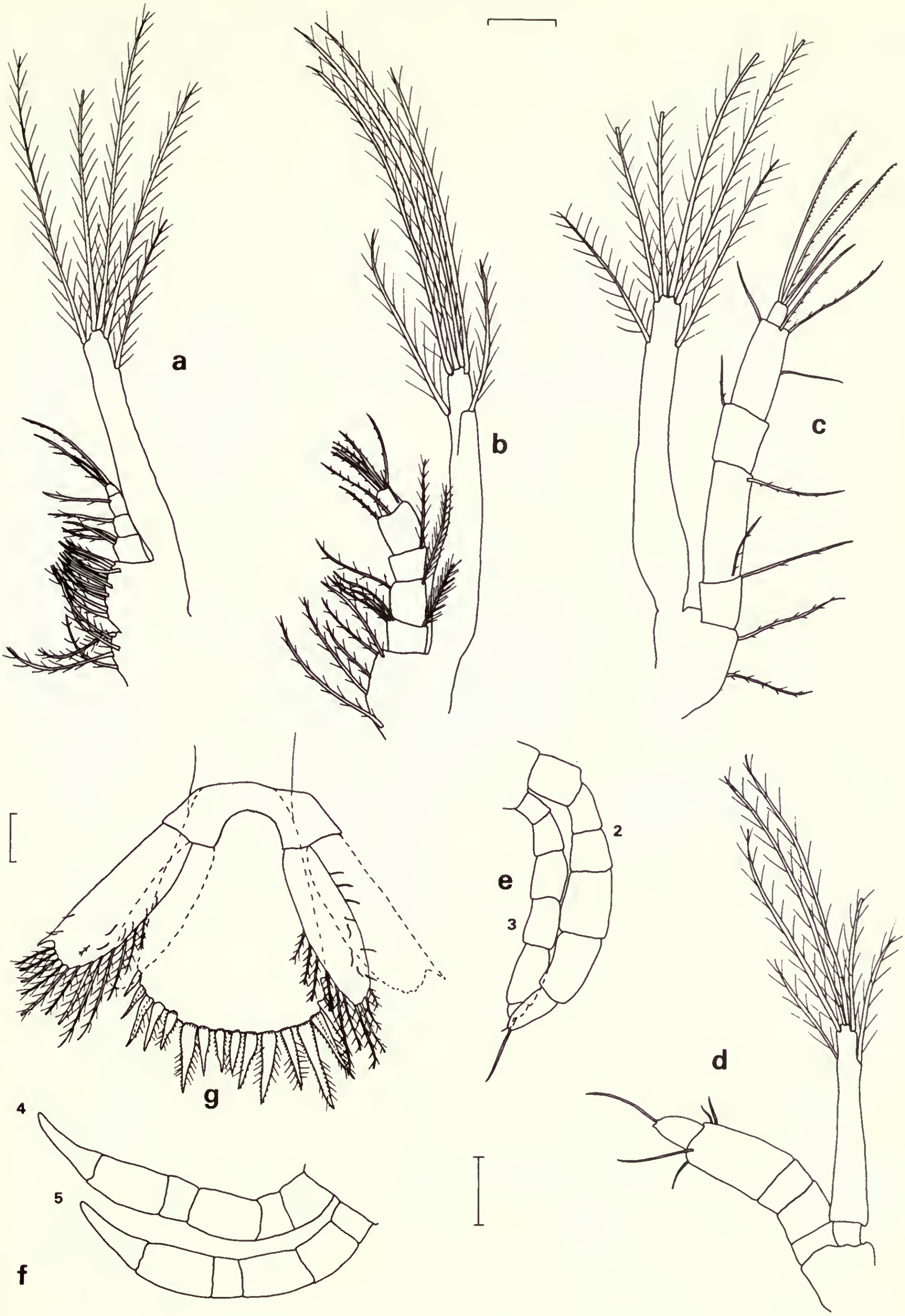

Fig. 9 Zoea 6: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopods 2 & 3; (f) pereiopods 4 & 5; (g) telson.
Bar scales: a–g = 0·1 mm.

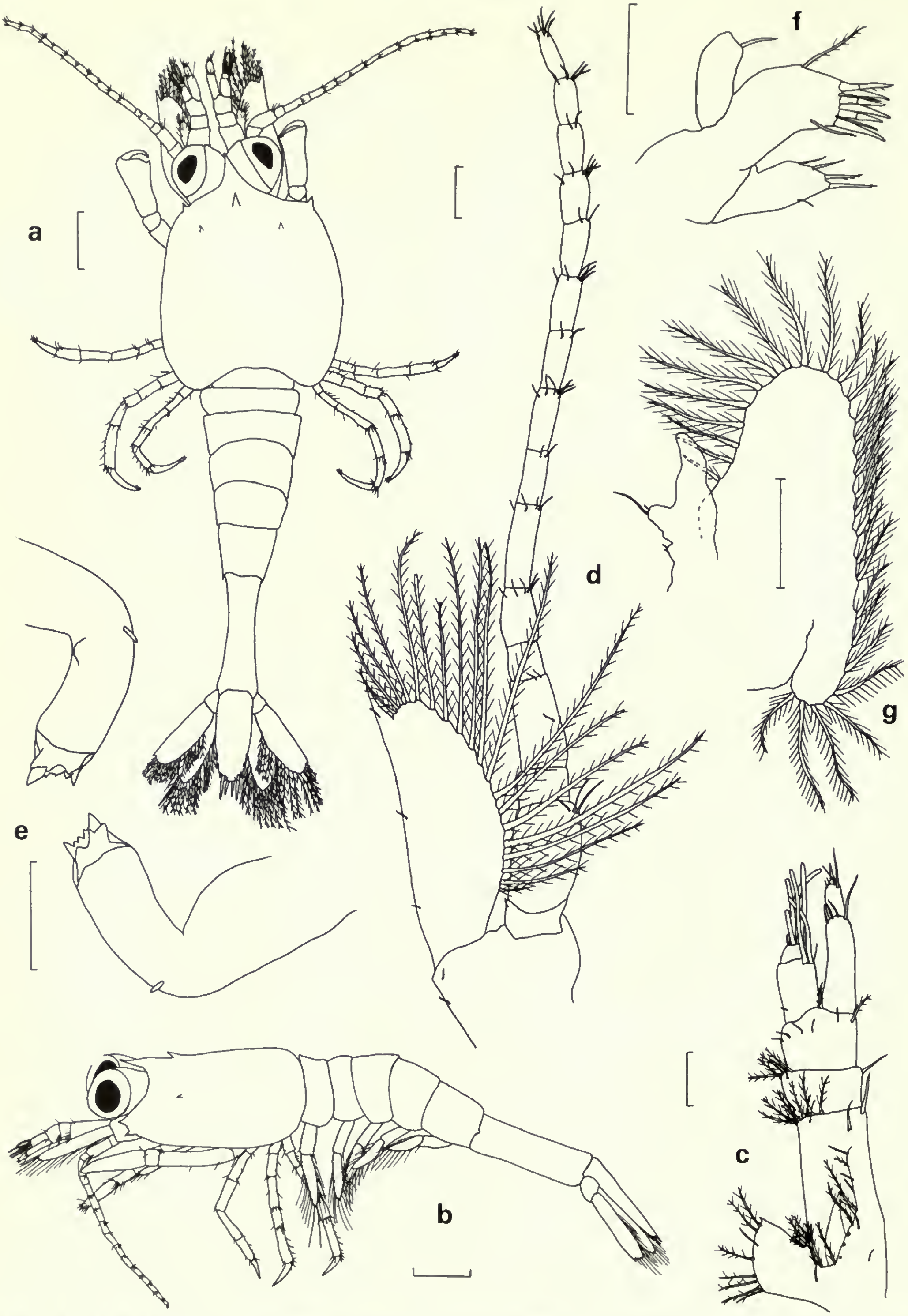

Fig. 10 Post Larva 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2.
Bar scales: a = 0·35 mm; b = 0·4 mm; c–g = 0·1 mm.

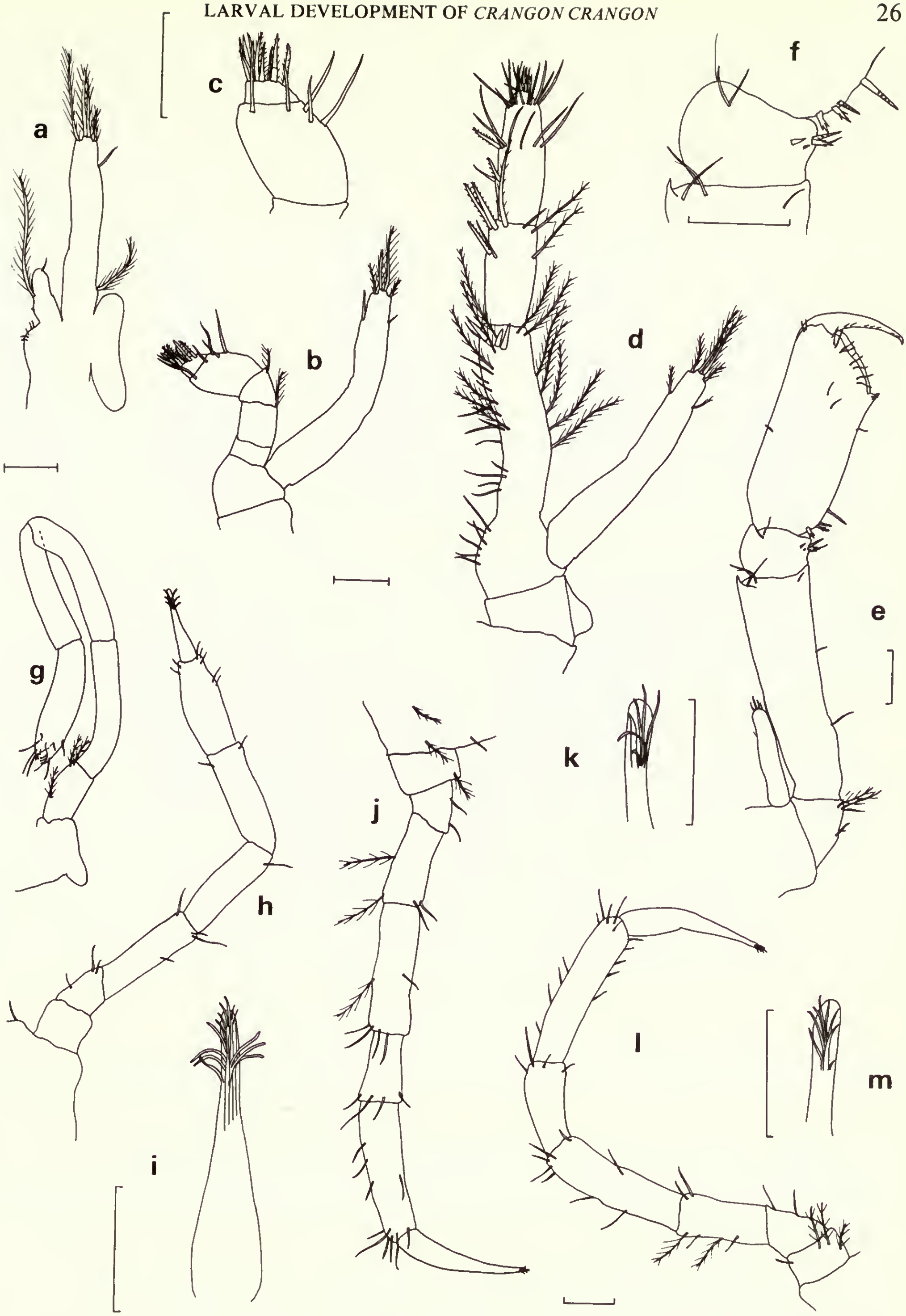

Fig. 11 Post Larva 1: (a) maxilliped 1; (b) maxilliped 2; (c) detail of endopod of maxilliped 2; (d) maxilliped 3; (e) pereiopod 1; (f) detail of pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) detail of terminal segment pereiopod 3; (j) pereiopod 4; (k) detail of terminal segment pereiopod 4; (l) pereiopod 5; (m) detail of terminal segment pereiopod 5.
Bar scales: a–m = 0·1 mm.

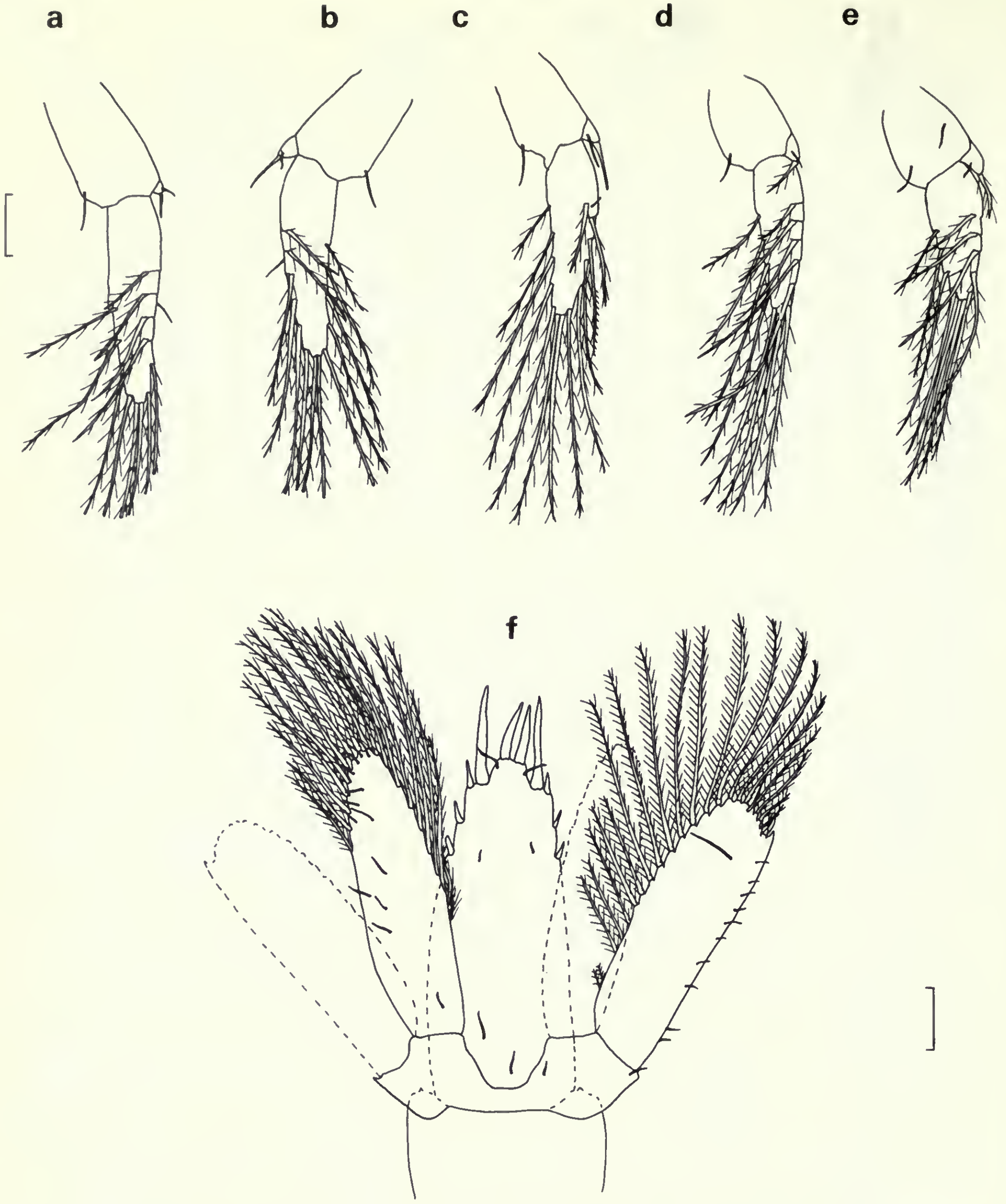

Fig. 12 Post Larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) telson.
Bar scales: a–f = 0·1 mm.

A revision of the spider genus *Cocalodes* with a description of a new related genus (Araneae: Salticidae)

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Introduction

The genus *Cocalodes* Pocock, 1897, known from Amboina, Seram, Halmahera and New Guinea, is comprised of 12 species, six of which are described here as new. Petrunkevitch (1928) placed *Cocalodes* in the subfamily Boethinae, but as far as I am aware it shows no close affinities with the nominate genus *Boethus* or related genera (sensu Wanless, 1981). It is, however, closely allied to *Allococalodes* gen. n., proposed here for two new taxa from New Guinea.

Both genera are unique in that the majority of males possess a well developed median horn arising from a sclerite between the lower basal margins of the chelicerae (Figs 8A, 21B). This structure has not been described in *Cocalodes* by earlier authors, for in the majority of species it does not protrude beyond the edge of the clypeus and is readily overlooked. The horn is not homologous with the paired horns of *Padilla* Peckham & Peckham, which arise from the basal region of the anterior surface of the chelicerae. Neither is it homologous with the horn of *Thorellia* Keyserling which arises from the clypeus.

The male palps of both *Cocalodes* and *Allococalodes* are also of interest in possessing a functional conductor and median apophysis which seldom occur in other Salticidae. In *Allococalodes* the functional conductor and median apophysis are lobe-like (Fig. 16E) and relatively simple when compared with the elaborate fan-like functional conductor and bifid median apophysis characteristic of *Cocalodes* (Fig. 6G). The less complex structures of *Allococalodes* are possibly vestigial or germinal in respect of those of *Cocalodes*, but for the present it is a matter for conjecture as the affinities of both genera are uncertain.

The standard abbreviations and measurements are those used by Wanless (1978), but for the leg spination the system is that used by Platnick and Shadab (1975).

Genus *COCALODES* Pocock

Cocalodes Pocock, 1897 : 627. Type species *Cocalodes leptopus* Pocock, by original designation. Simon, 1901 : 400, 403–405. Waterhouse, 1902 : 80. Petrunkevitch, 1928 : 181. Neave, 1939, I : 778. Roewer, 1954 : 936. Bonnet, 1956 : 1172.

DEFINITION. Small or large spiders ranging from about 4·5 to 11·0 mm in length. Most species elongate and narrow with long slender legs, the abdomen usually marked with characteristic dark lateral bands; chelicerae robust, in males usually elongate and porrect with a median horn which sometimes protrudes beyond the clypeus; not hirsute, fringes lacking.

Carapace: longer than broad, moderately high, widest at about level of coxae II–III; fovea long, weakly sulciform, positioned more or less midway between posterior margins of posterior lateral eyes. *Eyes*: with black surrounds except anterior medians; posterior medians and posterior laterals on moderately well developed tubercles;

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arranged in three transverse rows, comprised of anterior medians (AM) and anterior laterals (AL), posterior medians (PM), and posterior laterals (PL); anteriors more or less contiguous with apices procurved in frontal view and recurved in dorsal view; anterior medians largest; anterior laterals greater than half diameter of anterior medians; posterior medians relatively large, positioned closer to and on or slightly outside optical axis of anterior lateral eyes; posterior laterals as large or slightly smaller than anterior laterals and set inside lateral margins of carapace when viewed from above; quadrangle formed by posterior median and posterior lateral eyes broader than long and wider behind; entire quadrangle, measured from between bases of anterior medians to posterior margins of posterior laterals, occupying between 47 and 60 per cent of carapace length. *Clypeus*: between 18 and 42 per cent of diameter of anterior median eyes. *Chelicerae*: robust, slightly diverging and inclined anteriorly in females; in males usually elongate, diverging and porrect with median horn of variable length which arises from between the lower margins of the cheliceral bases (Fig. 21B); pro- and retromargins usually with three teeth. *Maxillae*: long and diverging with rounded apices. *Labium*: oblong, generally less than half maxillae length. *Sternum*: more or less as in Figs 3B, 14G; slightly elongate scutiform. *Coxae*: I and II generally larger than III–IV. *Pedicel*: short. *Abdomen*: long slender and tapering; spinnerets moderately long, posteriors longest with long apical articles, anteriors robust, slightly longer than more slender medians; spiracle a transverse slit just in front of anterior spinnerets; tracheal system not examined; position of colulus indicated by scant group of hairs; anal tubercle cone-shaped. *Legs*: long and slender; spines strong and numerous; claws pectinate; tufts present; scopulae absent. *Female palps:* long and slender with apical claw. *Male palps*: moderately complex, intra- and generally interspecifically distinct. Femora long and bowed; patellae long; tibiae long with broad retrolateral or ventral apophysis; cymbium with hair tuft protecting embolic tip (Fig. 2H), distal finger-like extension, swelling on retrolateral basal margin and usually a group of peg-like spines on dorsal basal margin (Figs 1A; 18A); embolus (e) very long and slender, sometimes thread-like, resting distally in well developed membraneous fan-like functional conductor (c), the tip of which ends in a sclerotized spur; a bifid median apophysis arises from a translucent pleated membrane on the tegulum (Figs 1B; 4H); tegulum (t) irregular in form with seminal ducts; median hematodocha in form of a membraneous sac between tegulum and subtegulum only evident in fully expanded palps; subtegulum (st) a sclerotized ring at distal end of basal hematodocha (bh). *Epigynes*: of various forms; median septum sometimes present and occasionally bearing lateral pouches; introductory ducts long, simply looped or convoluted, of variable width, sometimes narrow (Fig. 8G, H), or sac-like (Figs 4F, G; 6F) or resembling spermathecae (Fig. 141, J); spermathecae of various shapes with leaf-like fertilization ducts; spherical objects frequently present in interstitial spaces (Fig. 21C–F).

AFFINITIES. The general habitus, presence of a median cheliceral horn, functional conductor and median apophysis suggest that *Cocalodes* and *Allococalodes* are closely related, even sister groups. Both genera are also probably allied to *Holcolaetis* Simon, from Africa and *Sonoita* Peckham & Peckham from South Africa, as the male papal organs evidently possess an homologous conductor and median apophysis.

DIAGNOSIS. Males of *Cocalodes* are readily distinguished from other Oriental salticids by the distinctive palpal organs. Females are separated with more difficulty by the geographical distribution, relatively large posterior median eyes, by the structure of the epigynes and by having three teeth on the posterior margin of the chelicerae. A more useful diagnosis or assessment of affinities cannot be given until supposedly related genera have been revised.

REMARKS. 1. The sclerite from which the median horn arises in *Cocalodes* and *Allococalodes* has not been routinely examined in previous revisions and not even in all females of *Cocalodes* in the present study, as the chelicerae have to be displaced or detatched from the carapace to expose it. A cursory examination of several Salticidae suggests that the sclerite is present in all members of the family. It is usually seen as

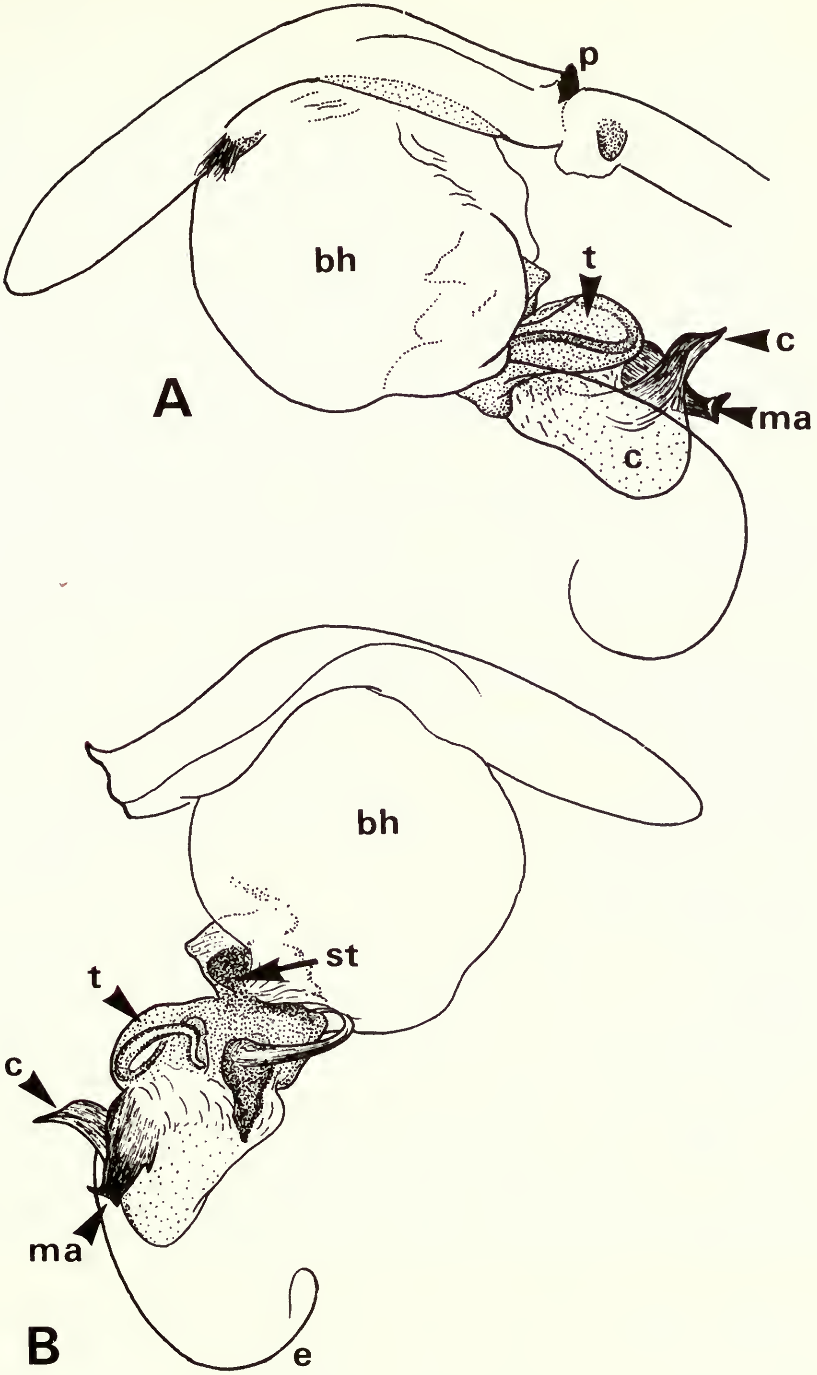

Fig. 1 *Cocalodes papuanus* Simon. Expanded ♂ palp: A, retrolateral; B, prolateral. Abbreviations: bh, basal hematodocha; c, functional conductor; e, embolus; ma, median apophysis; p, peg-like cymbial spines; st, subtegulum; t, tegulum.

an indistinct elongate plate embedded in tissue between the bases of the lower margins of the chelicerae. In females of *Cocalodes thoracicus* Szombathy and in males and females of *Holcolaetis* it forms a peg-like horn similar to that of *C. papuanus* Simon (Fig. 21B). This does not, however, necessarily support a relationship between *Holcolaetis* and *Cocalodes* as our knowledge of the development of this sclerite is inadequate.

2. The spherical objects found clustered or irregularly distributed in the interstitial spaces of the epigynes of most female *Cocalodes* vary in diameter from 8 to 20 μ. Sometimes they can be seen through the cuticle of intact epigynes (Fig. 14H), but they are most readily observed in epigynes which have been cleared in lactic acid (Figs 20F; 21C–F). When examined by transmitted light microscopy most spheres appear to have a refractile centre, but with interferance microscopy, the centres are transformed into surface depressions which resemble a lunar crater with indistinct lines radiating outwards from the raised margins (Fig. 21F). Some spheres appear to have collapsed and look ragged with irregular and illdefined craters.

These objects, which are not known to occur in other Salticidae, resemble the unidentified spheres described by Forster (1980) from the epigyne of a *Gamasomorpha* species (Family Oonopidae). A concensus of opinion (Forster, 1980) favoured a sporozoan infection, but this seems unlikely in the present case as the spheres lack the rod-like structures illustrated by Forster, furthermore their presence in almost every female of a wide range of species suggests they are a natural feature of these epigynes, which could be associated with spermatogenisis, oviposition or even plugging. Clearly, they require further investigation.

Lists of species in the genus *Cocalodes* Pocock, 1897

Cocalodes cygnatus sp. n.
C. expers sp. n.
C. innotabilis sp. n.
C. leptopus Pocock, 1897
C. longicornis sp. n.
C. longipes (Thorell, 1881)
C. macellus (Thorell, 1878)
C. papuanus Simon, 1900
C. platnicki sp. n.
C. protervus (Thorell, 1881)
C. turgidus sp. n.
C. thoracicus Szombathy, 1915

The species of *Cocalodes* could on the basis of the development of the epigynal septum be divided into two groups. However, these groups have not been proposed as there does not appear to be any correlation with characters of the male palpal organs. This may be a natural phenomenon or the result of incorrectly matching males and females. Matching the sexes has been difficult in the present study and where doubts have existed, these are mentioned in the species descriptions. As is often the case, additional material should resolve many of these problems.

Key to species of *Cocalodes*

Males (the males of *expers, protervus* and *turgidus* are unknown)

1 Dorsal prong of median apophysis broad and distally truncate (Fig. 2C, F); chelicerae with dorsal cluster of stout bristles (Fig. 2A) . . . . **papuanus** Simon (p. 267)
– Dorsal prong of median apophysis otherwise; chelicerae lacking stout bristles . . . 2
2 Peg-like cymbial spines present (Figs 4C; 18A) 3

– Peg-like cymbial spines absent 8
3 Conductor tip cygniform (Fig. 6G) . . . . **cygnatus** sp. n. (p. 273)
– Conductor tip otherwise 4
4 Dorsal and ventral prongs of median apophysis more or less equal in length (Fig. 10C, D) . . . . **thoracicus** Szombathy (p. 280)
– Dorsal prong of median apophysis much longer than ventral prong 5
5 Dorsal prong of median apophysis finger-like or scimitar-shaped (Figs 13C, E; 15D, E) 6
– Dorsal prong of median apophysis acuminate (Figs 4C; 7H, I) 7
6 Conductor tip forming a triangular plate (Fig. 13G); dorsal prong of median apophysis scimitar-shaped (Fig. 13E) . . . . **longipes** (Thorell) (p. 284)
– Conductor tip otherwise (Fig. 15F); dorsal prong of median apophysis finger-like (Fig. 15D, E) . . . . **innotabilis** sp. n. (p. 288)
7 Conductor tip slender with minute barb (Fig. 7G, I) . . . . . **macellus** (Thorell) (p. 275)
– Conductor tip robust, barb lacking (Fig. 4H) . . . . . . **leptopus** Pocock (p. 270)
8 Dorsal prong of median apophysis relatively slender (Fig. 14D, E); cheliceral horn not protruding beyond clypeal margin . . . . **platnicki** sp. n. (p. 286)
– Dorsal prong of median apophysis relatively robust (Fig. 8B, C); cheliceral horn protruding well beyond clypeal margin (Fig. 8A, D) . . . . . **longicornis** sp. n. (p. 277)

Females (the female of *innotabilis* is unknown)

1 Epigyne with median septum 2
– Epigyne lacking median septum 7
2 Epigyne with relatively large openings (Fig. 3D) . . . . . . **papuanus** Simon (p. 267)
– Epigyne with relatively small openings 3
3 Epigynal septum narrow and not extending to posterior margin (Fig. 7C) . . . 4
– Epigynal septum broad, extending to posterior margin 6
4 Clypeus white haired; epigynal openings more or less ovoid in outline (Figs 9B, 7C) 5
– Clypeus not white haired; epigynal openings indistinct (Fig. 8F) . . **longicornis** sp. n. (p. 277)
5 Spermathecae large and dark (Fig. 9B) . . . . **protervus** (Thorell) (p. 279)
– Spermathecae small and pale, hardly if at all visible through integument (Fig. 7C, D) . . . . **macellus** (Thorell) (p. 275)
6 Epigynal septum with median bulge (Fig. 12B) . . . . **turgidus** sp. n. (p. 283)
– Epigynal septum lacking median bulge (Fig. 11B, C) . . . . **thoracicus** Szombathy (p. 280)
7 Epigyne with small median openings and broad posterior ledge (Fig. 14H) **platnicki** sp. n. (p. 286)
– Epigyne otherwise 8
8 Epigyne slightly depressed with comma-shaped introductory ducts (Fig. 13B) . . . **longipes** (Thorell) (p. 284)
– Epigyne otherwise 9
9 Epigyne with deep median notch on posterior margin (Fig. 5C) . . . . **expers** sp. n. (p. 271)
– Epigyne otherwise 10
10 Epigyne with two notches on posterior margin (Fig. 6D) . . . . . **cygnatus** sp. n. (p. 273)
– Epigyne without notches on posterior margin (Fig. 4E) . . . . . **leptopus** Pocock (p. 270)

Cocalodes papuanus Simon
(Figs 2A–H; 3A–E; 18C, E; 19A, B; 21B)

Cocalodes papuanus Simon, 1900 : 32, ♂. LECTOTYPE ♂ (here designated) Irian Jaya (MNHN, Paris) [examined]. Simon, 1901 : 403–404. Roewer, 1954 : 936. Bonnet, 1956 : 1173. Prószyński, 1971 : 390.

Cocalodes armatissimus Strand, 1913 : 122, ♂. LECTOTYPE ♂ (here designated) Schouten Island (FS, Frankfurt am Main) [examined]. Strand, 1915 : 262. Roewer, 1954 : 936. Bonnet, 1956 : 1172. Prószyński, 1971 : 390. **Syn. n.**

Cocalodes plebejus Szombathy, 1915 : 468, ♂, ♀, immatures. Syntypes (presumably in TM, Budapest) [not examined]. Roewer, 1954 : 936. Bonnet, 1956 : 1173. **Syn. n.**

REMARKS. Szombathy (1915) supplied good figures of the palpal organs in his original description of *C. plebejus* and there is little doubt that *plebejus* and *papuanus* are conspecific.

DIAGNOSIS. Separated from other species of *Cocalodes* by the cluster of cheliceral setae and truncate median apophysis (Fig. 2C, F) in males, and by the large rounded epigynal openings in females (Fig. 3D).

MALE from Madang, Papua New Guinea. In good condition. *Carapace* (Fig. 2A, B): pale yellow-brown grading to orange-brown in eye region with dark brown bands around margins and from PL's to posterior margin of thorax; pale areas clothed in creamy white hairs with orange-brown or black hairs elsewhere. *Eyes*: with black surrounds except AM; fringed in creamy white and pale amber hairs. *Clypeus*: clothed in very fine whitish hairs. *Chelicerae*: elongate, porrect and diverging; orange-brown with dorsal cluster of stout spines; shiny under some angles of illumination; promargin with four teeth, retromargin with two; cheliceral horn small, not protruding beyond clypeal margin. *Maxillae and labium*: pale yellow grading to whitish yellow along inner margins of maxillae. *Sternum*: more or less as in female; pale yellow, shiny. *Coxae*: pale yellow to whitish yellow with black lateral bands on coxae I. *Abdomen*: pale yellow with sooty markings and blackish lateral bands above, greyish black below; clothed in fine iridescent setae; spinnerets pale yellow heavily tinged grey-black except for whitish medians. *Legs*: legs I pale yellow to amber with blackish lateral markings on femora and metatarsi; legs II similar, but lighter with less conspicuous dark markings; legs III pale yellow grading to light amber distally; legs IV as III, but with black lateral markings on patellae, tibiae and metatarsi; spines numerous, strongest on legs I. Spination of legs I: metatarsi v 2–2–2, p 1–0–1, r 1–0–1; tibiae v 2–2–2, p 1–1–1, r 1–1–1, d 1–0–1; patellae 1–0–0, r 1–0–0; femora p 1–1–1, d 1–1–3, r 1–2–1. *Palp* (Figs 2C, E, F, H; 18C, E): the truncate dorsal prong of the median apophysis and pronounced functional conductor are characteristic of this species.

Dimensions (mm): total length 7·88; carapace length 3·02, breadth 2·22, height 1·44; abdomen length 4·84; eyes, anterior row 1·96, middle row 1·68, posterior row 1·68; quadrangle length 1·6 (52% of carapace length). *Ratios*: AM : AL : PM : PL :: 16 : 9 : 6 : 9; AL–PM–PL :: 10–13; AM : CL (clypeus) :: 16 : 3 (18% of AM diameter).

FEMALE (formerly undescribed) from Madang, Papua New Guinea. In good condition. *Carapace* (Fig. 3A): pale yellow-brown, shiny; clothed in fine whitish hairs with bands composed of amber hairs from posterior lateral eyes to posterior thoracic margin. *Eyes*: as in ♂. *Clypeus*: below anterior median eyes and inner sides of anterior laterals fringed in pale amber hairs with outer sides of anterior laterals densely white haired. *Chelicerae*: robust, porrect and diverging; yellow-brown, shiny; thinly clothed in yellow-brown hairs; both margins with three teeth. *Maxillae and labium*: pale yellow, shiny. *Sternum* (Fig. 3B): pale yellow, shiny. *Coxae*: pale yellow, shiny. *Abdomen*: whitish yellow; irregularly clothed (?partly rubbed) in very fine iridescent setae with longitudinal bands, composed of dark amber hairs, flanked externally by white haired bands on the sides; spinnerets pale yellow tinged grey. *Legs*: pale yellow-brown with blackish lateral streaks on metatarsi IV. Spination of legs I: metatarsi v 4–0–2, p 1–0–1, r 1–0–1; tibiae v 2–3–1, p 1–1–1, r 1–1–1, d 1–0–1; patellae p 1–0–0, r 1–0–0; femora p 0–2–1, d 1–1–2, r 1–2–1. *Epigyne* (Figs 3C–E; 19A, B): clothed in testaceous hairs.

Dimensions (mm): total length 10·8; carapace length 3·76, breadth 2·8, height 1·64; abdomen length 6·8; eyes, anterior row 2·26, middle row 1·96, posterior row 1·96; quadrangle length 1·8 (47% of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 10 : 5·5 : 10; AL–PM–PL :: 11–16; AM : CL :: 19 : 5 (26% of AM diameter).

VARIATION. ♂ total length varies from 4·88 to 10·4 mm, carapace length 2·6–3·96 mm (seven specimens). ♀ total length 8·48–10·8 mm, carapace length 2·92–3·76 mm (three specimens).

In males the number of peg-like spines on the cymbium varies from two to four. In one specimen (lectotype of *C. papuanus*) the left palp has two spines on the cymbium while the right has three. In females the epigyne varies slightly, the dorsal rims of the rounded openings sometimes lie across the posterior margins of the spermathecae.

DISTRIBUTION. Papua New Guinea; Irian Jaya.

MATERIAL EXAMINED. **Papua New Guinea**: Madang Province, Madang, 22.iii.1979 (*H. W. Levi, Y. Lubin, B. Robinson*) (MCZ, Harvard): 1♀, garden, night collection; 1♂, 40 Km S. of Madang, swamp forest. Astrolabe Bay: (*R. Rohde*) (MNHU, Berlin. 17795). **Irian Jaya**: Dorey, Lectotype ♂, (*A. Raffray*) (MNHN, Paris. 5479); Schouten Island,

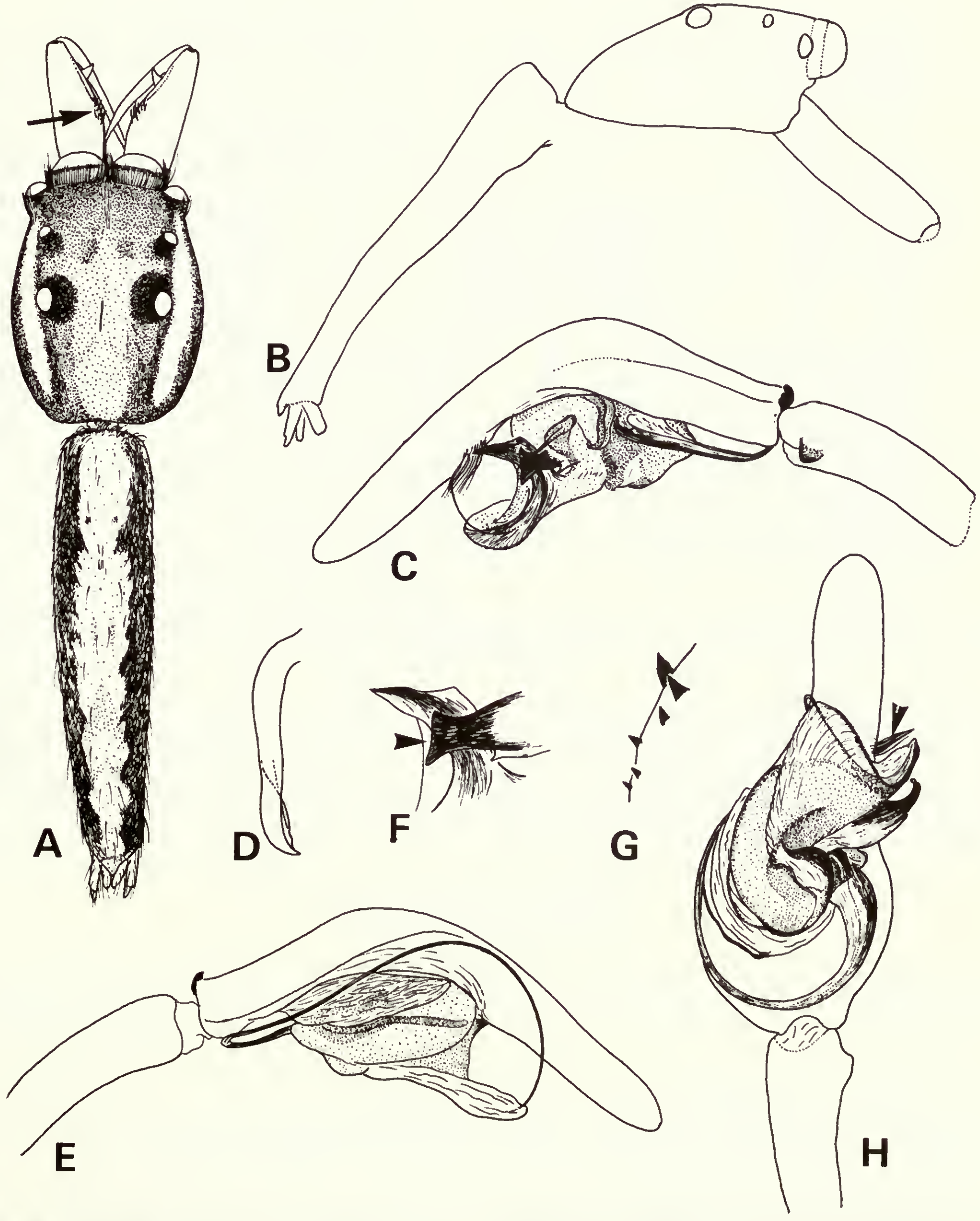

Fig. 2 *Cocalodes papuanus* Simon. ♂: A, dorsal; B, lateral; C, palp, retrolateral; D, cleared fang; E, palp, prolateral; F, median apophysis and tip of functional conductor; G, cheliceral teeth inner view; H, palp, ventral.

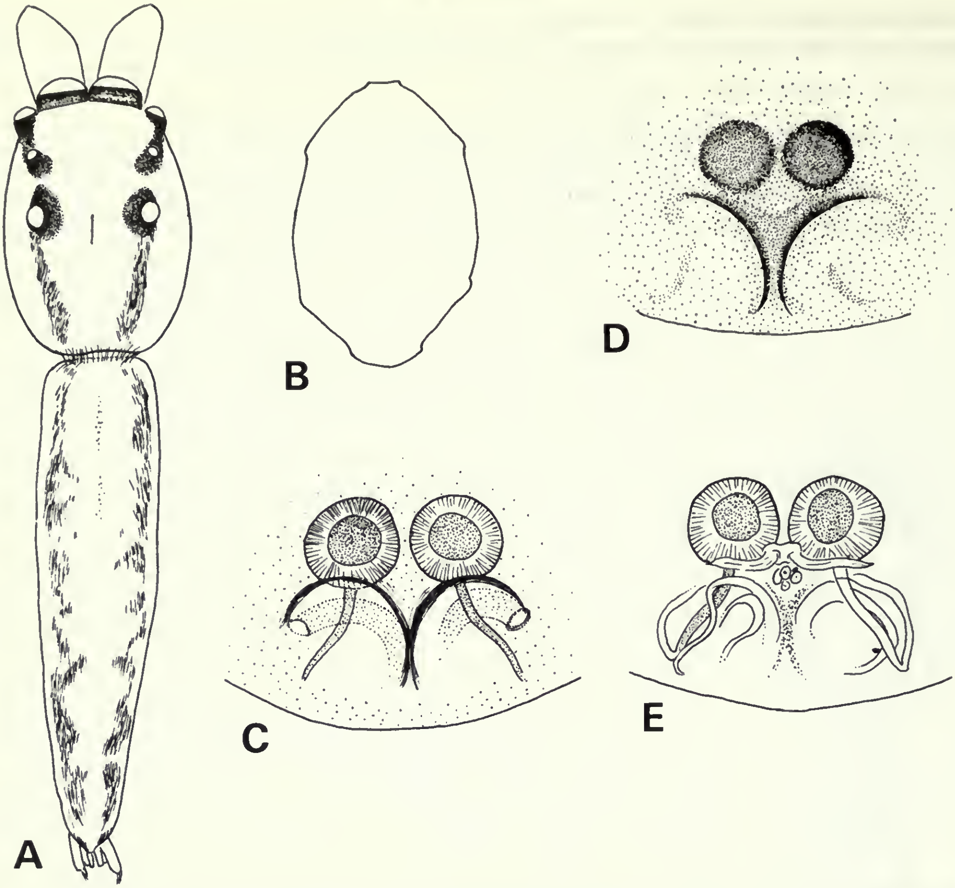

Fig. 3 *Cocalodes papuanus* Simon. ♀: A, dorsal; B, sternum; C, vulva ventral; D, epigyne; E, vulva, dorsal.

Woges, [lectotype ♂ of *C. armatissimus*], 1909, (*E. Wolf*) (FS, Frankfurt am Main. 2431). Sukarnapura (Hollandia) AMNH, New York): 1♂, v. 1945 (*Borys Malkin*); 1♀, rainforest, 250 ft. xii. 1944 (*H. Hoogstraal*); 1♂, on foliage, rainforest, 300 ft. xii.1944 (*L. W. Saylor*). Sukarnapura: 2♂, 1936 (*L. E. Cheeseman*) (BMNH. 1937.12.13.117); 1♀, 1936 (*L. E. Cheeseman*) (BMNH. 1937.12.13.161).

Cocalodes leptopus Pocock
(Figs 4A–H; 19C, D)

Cocalodes leptopus Pocock, 1897 : 628, ♀. Holotype ♀, Indonesia (BMNH) [examined]. Simon, 1901 : 403–405. Petrunkevitch, 1928 : 181. Roewer, 1954 : 936. Bonnet, 1956 : 1172. Prószyński, 1971 : 390.

Cocalodes melanognathus Pocock, 1897 : 629, ♂. Holotype ♂, Indonesia (BMNH) [examined]. Simon, 1901 : 403–404. Roewer, 1954 : 936. Bonnet, 1956 : 1172. Prószyński, 1971 : 390. **Syn. n.**

REMARKS. As *C. leptopus* and *C. melanognathus* both originate from Halmahera and are only known from separate sexes, they are regarded here as being conspecific.

DIAGNOSIS. From females of *C. cignatus* and *C. expers* by the apparent absence of a notch or notches on the posterior margin of the epigynal plate (Fig. 4E). From male *cygnatus* by the lack of a white moustache below the anterior median eyes and by the curved tip of the functional conductor (Fig. 4H). Males of *expers* are unknown.

FEMALE HOLOTYPE. In poor condition. *Carapace*: brown-black with orange-brown eye region; irregularly clothed in whitish hairs, especially dense below lateral eyes. *Eyes*: with black surrounds; irregularly fringed in whitish hairs. *Clypeus*: densely white haired. *Chelicerae*: robust, inclined anteriorly and slightly diverging; brown with lighter brown markings; pro- and retromargins with three teeth. *Maxillae* (Fig. 4D): brownish orange grading to yellow-brown along inner margins. *Labium*: brownish orange tipped yellow-brown. *Sternum*: greenish yellow with thin brownish margins; shiny. *Coxae*: dark grey tinged greenish yellow. *Abdomen*: greenish yellow with brownish lateral markings and two pairs of impressed spots dorsally; clothed in whitish hairs (mostly rubbed on dorsum) with irregular longitudinal red haired bands on each side; spinnerets greenish yellow tinged black. *Legs*: brownish orange tinged greyish green, femora IV and patellae IV with black spots; spines strong and numerous. Spination of legs I: metatarsi v 2–0–0, p 1–1–1, d 0–0–2, r 1–1–1; tibiae v 4–4–4; patellae p 1–0–0, r 1–0–0; femora p 1–0–2, d 0–2–2, r 0–1–1. *Epigyne* (Figs 4E–G; 19C, D): a low dark mound with indistinct lateral openings (arrowed in Fig. 4F).

Dimensions (mm): total length 10·0; carapace length 3·56, breadth 3·0, height 2·24; abdomen length 6·56; eyes, anterior row 2·52, middle row 2·12, posterior row 2·16; quadrangle length 1·92 (53% of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 11 : 7 : 10; AL–PM–PL :: 13–15; AM : CL :: 19 : 9 (47% of AM diameter).

MALE (holotype of *C. melanognathus*). In poor condition. *Carapace* (Fig. 4A, B): dark chocolate brown with orange-brown eye region; badly rubbed. *Eyes*: with black surrounds except AL and AM. *Clypeus*: irregularly and scantily clothed in fine whitish hairs. *Chelicerae*: elongate, porrect and diverging; dark brown with bluish sheen under some angles of illumination; pro- and retromargins with three teeth; horn small, dislocated by a pin pushed through the specimen, a method frequently used by Pocock for orientating larger spiders. *Maxillae, labium, sternum and coxae*: more or less as in ♀. *Abdomen*: similar to ♀. *Legs*: broken and detached, otherwise similar to ♀. *Palp* (Fig. 4C, H): similar to that of *C. cygnatus*, but readily distinguished by the curved tip of the functional conductor.

Dimensions (mm): total length 8·8; carapace length 3·4, breadth 2·72, height 2·08; abdomen length 5·36; eyes, anterior row 2·48, middle row 2·08, posterior row 2·16; quadrangle length 1·94 (57% of carapace length). *Ratios*: AM : AL : PM : PL :: 19·5 : 11·5 :: 7 : 11; AL–PM–PL :: 12–15; AM : CL ::19·5 : 5 (28% of AM diameter).

DISTRIBUTION. Indonesia: Halmahera.

MATERIAL EXAMINED. **Halmahera**: Patani, holotype ♀, ii.1894 (*Kükenthal*); Soah Konorah, holotype ♂ [of *C. melanognathus*] 1894 (*Kükenthal*) (BMNH. 1981.1.22.1–2.)

Cocalodes expers sp. n.
(Fig. 5A–C)

DIAGNOSIS. From *C. leptopus* and *C. cygnatus* by the presence of a deep median notch on the posterior margin of the epigynal plate (Fig. 5C).

MALE. Unknown.

FEMALE HOLOTYPE. In good condition. *Carapace* (Fig. 5A, B): orange-brown with vague darker markings; irregularly clothed in short, fine shinning hairs which appear whitish or pale amber under varying angles of illumination. *Eyes*: with black surrounds except AM; fringed in whitish and pale amber hairs. *Clypeus*: densely clothed in creamy white hairs. *Chelicerae*: robust, divergent and inclined anteriorly; orange-brown, thinly clothed in clear amber hairs; pro- and retromargins with three teeth. *Maxillae and labium*: amber, shiny. *Sternum*: light amber with darker margins; thinly covered in light brownish

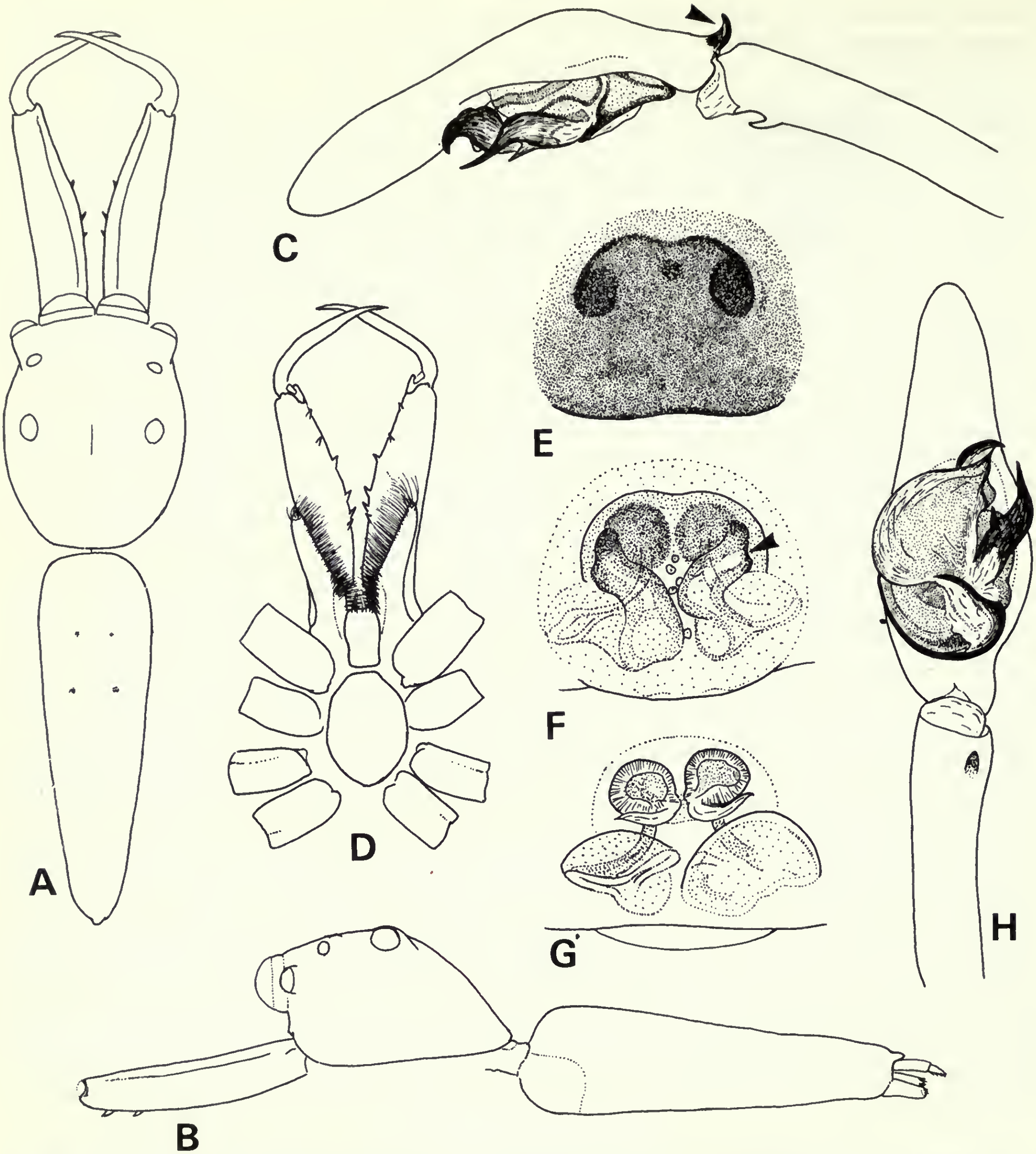

Fig. 4 *Cocalodes leptopus* Pocock. ♂ (holotype of *C. melanognathus*): A, dorsal; B, lateral; C, palp, retrolateral; H, palp, ventral. Holotype ♀: D, sternum, coxae and mouth parts; E, epigyne; F, vulva, ventral; G, vulva, dorsal.

hairs. *Coxae*: light amber. *Abdomen*: pale orange-brown with fine shinning hairs, scattered spots composed of amber hairs, and dark reddish brown lateral bands covered in dark amber hairs; spinnerets pale orange-brown. *Legs*: orange-brown with blackish apices on femora IV; spines numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–1, r 1–0–1; tibiae v 2–2–2, p 1–1–1, d 0–1–0, r 1–1–1; patellae p 0–1–0, r 0–1–0; femora p 2–2–1, d 1–1–3, r 2–1–1. *Epigyne* (Fig. 5C): similar to that of *C. leptopus*, but readily separated by the median notch on the posterior margin of the epigynal plate.

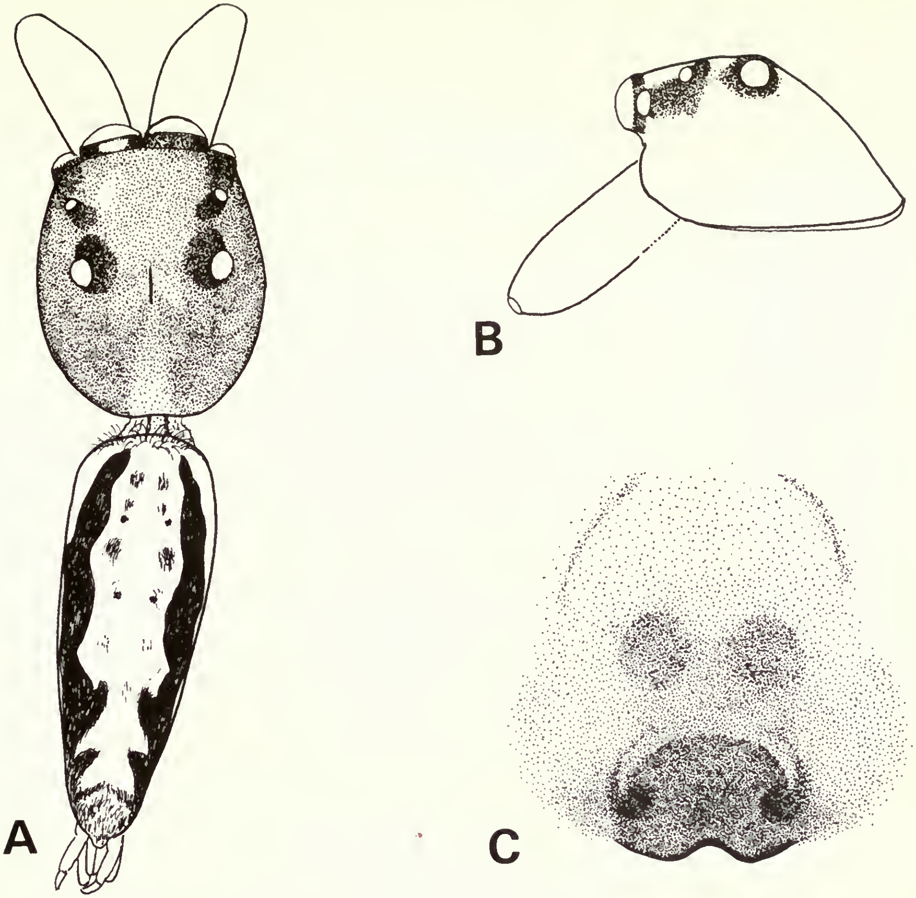

Fig. 5 *Cocalodes expers* sp. n. Holotype ♀: A, dorsal; B, carapace lateral; C, epigyne.

Dimensions (mm): total length 10·9; carapace length 4·5, breadth 3·8, height 2·8; abdomen length 6·24; Eyes, anterior row 3·04, middle row 2·68, posterior row 2·68; quadrangle length 2·28 (50% of carapace length). *Ratios:* AM : AL : PM : PL :: 22 : 14 : 8 :14; AL–PM–PL :: 14 : 19; AM : CL :: 22 : 8 (36% of AM diameter).

Distribution. Papua New Guinea.

Material examined. **Papua New Guinea**, D'Entrecasteaux Is., Fergusson Island, Iamelele about 1·5 miles from Seymour Bay, 15 m., camp 3. holotype ♀, 1956 (Fifth Archbold Exp. to New Guinea, *L. J. Brass*) (AMNH, New York).

Remarks. This species has been recorded from the same locality (Fergusson Island) as *C. longicornis* sp. n.

Cocalodes cygnatus sp. n.
(Figs 6A–G; 19E, F)

Diagnosis. From females of *C. leptopus* and *C. expers* by the presence of two small notches on the posterior margin of the epigynal plate (Fig. 6D). From male *leptopus* by the white moustache below the anterior median eyes and by the cygniform tip of the functional conductor (arrowed, Fig. 6G). Males of *expers* are unknown.

Male holotype. In fair condition. *Carapace* (Fig. 6A, B): orange-brown with dark

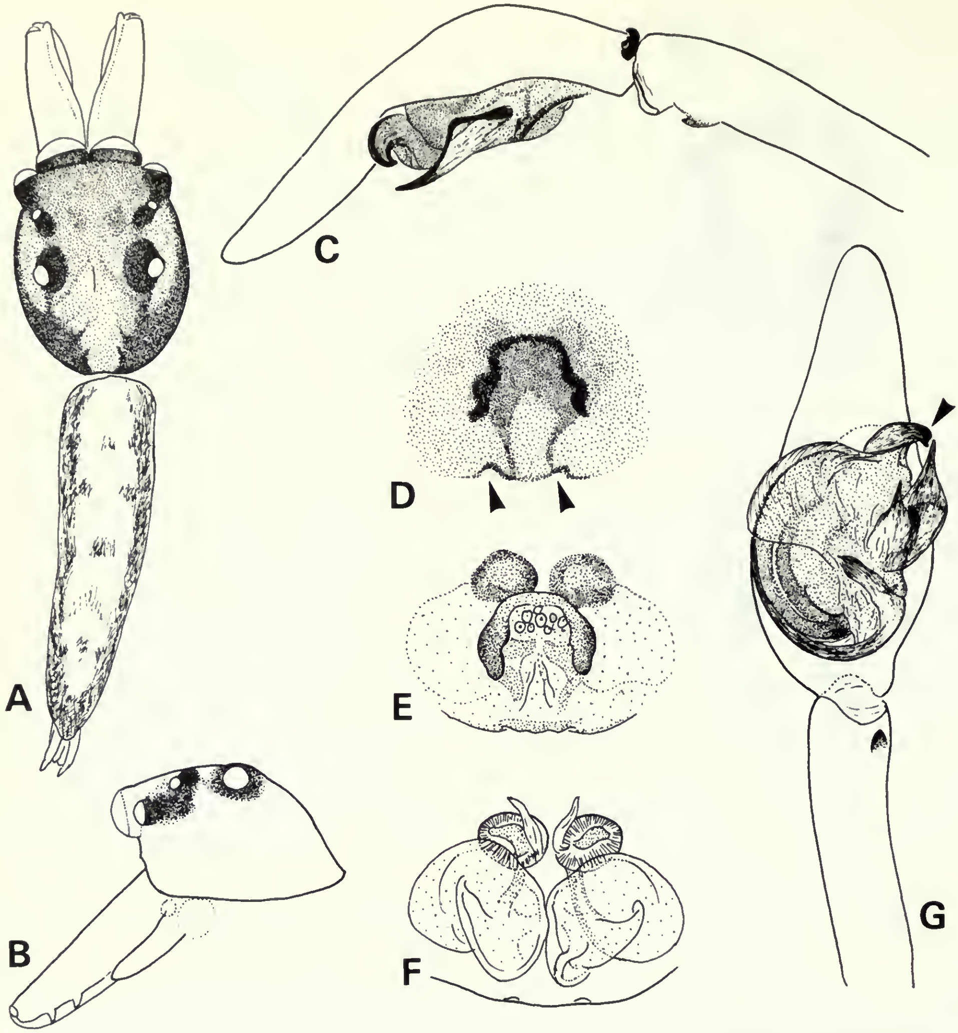

Fig. 6 *Cocalodes cygnatus* sp. n. Holotype ♂: A, dorsal; B, carapace, lateral; C, palp, retrolateral; G, palp, ventral. Paratype ♀: D, epigyne; E, vulva, ventral; F, vulva, dorsal.

brown margins and vague bands behind PL's; thinly clothed in whitish and pale amber hairs with scanty white haired patches on posterior declivity. *Eyes*: with black surrounds except AM; fringed by white hairs. *Clypeus*: densely white haired below AM. *Chelicerae*: elongate, porrect and diverging; dark reddish brown; shiny; thinly covered in pale amber hairs; pro- and retromargins with three teeth; horn small, not protruding beyond clypeal margin. *Maxillae*: brownish with inner margins orange-brown. *Labium*: dark brown tipped orange-brown. *Sternum*: yellow-brown with darker margins. *Coxae*: yellow-brown with black lateral stripes on coxae I. *Abdomen*: mottled grey-black with creamy white dorsal markings; spinnerets yellow-brown tinged black. *Legs*: legs I femora brown-black with yellow-brown markings, patellae and tarsi yellow-brown, tibiae dark brown with yellow-brown annuli, metatarsi basally yellow-brown grading to dark brown distally; other legs similar, but markings becoming paler except for brown-black blotches on femora IV: spines strong and numerous. Spination of legs I: metatarsi v 2–0–0, p 1–1–1, d 0–1–2, r 1–1–1; tibiae v 2–2–2, p 1–1–1, d 1–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 1–1–2, d 0–2–2, r 0–1–1. *Palp* (Fig. 6C, G): the tip of the functional conductor is sometimes obscured by the tip of the median apophysis. Also, in lateral view the ventral prong of the median apophysis is hardly evident, c.f. (*C. leptopus*).

Dimensions (mm): total length c. 8·2; carapace length 3·16, breadth 2·6, height 2·0; abdomen length 5·0; eyes, anterior row 2·36, middle row 1·98, posterior row 2·04; quadrangle length 1·84 (58% of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 11 : 5·5 : 10; AL–PM–PL :: 11–15; AM : CL :: 19 : 8 (42% of AM diameter).

Female paratype. In poor condition. *Carapace*: generally yellow-brown with blackish bands from PL's to thoracic margin; sparsely and irregularly clothed in creamy white hairs. *Eyes:* with black surrounds except AM; fringed in silky white hairs. *Chelicerae*: robust, diverging and inclined anteriorly; amber; shiny under some angles of illumination; with scattered pale amber hairs along inner margins; pro- and retromargins with three teeth. *Maxillae, labium, sternum and coxae*: yellow-brown. *Abdomen*: pale yellow-brown; clothed in fine whitish hairs with irregular lateral bands composed of amber hairs; spinnerets pale yellow-brown. *Legs*: generally yellow-brown, but with black spots on patellae IV and femora IV; spines strong and numerous on anterior legs becoming weaker and fewer on posteriors. Spination of legs I: metatarsi v 2–0–0, p 1–1–1, d 0–1–0, r 1–1–1; tibiae v 2–2–2, p 1–1–1, d 1–0–1, r 1–1–1; patellae r 1–0–0; femora p 1–1–1, d 0–2–3, r 0–1–1. *Epigyne* (Figs 6D–F;19E, F): a low mound as is *leptopus*, but pale and with more apparent detail.

Dimensions (mm): total length c. 8·0; carapace length 3·16, breadth 2·68, height 2·0; abdomen length 4·8; eyes, anterior row 2·44, middle row 2·07, posterior row 2·10; quadrangle length 1·88 (59% of AM diameter). *Ratios*: AM : AL : PM : PL :: 19 : 11·5 : 6 : 11; AL–PM–PL :: 12 : 15; AM : CL :: 19 : c. 8 (c. 42% of AM diameter).

Variation. Paratype ♂ measures c. 7·2 mm total length, 2·8 mm carapace length.

Distribution. Indonesia: Halmahera Island.

Material examined. **Halmahera Island**: Edkor, holotype ♂, paratype ♀ (MNHN, Paris. 7682). Paratype ♂, same data as holotype (BMNH, 1981.5.14.1).

Remarks. Simon misidentified the above specimens as *C. leptopus*, but as far as I am aware there has been no reference to them in the literature.

Cocalodes macellus (Thorell)

(Figs 7A–I; 20A, B)

Cocalus macellus Thorell, 1878 : 287, 311, ♀ and juvenile. Holotype ♀, juvenile, Amboina (MCSN, Genova) [examined]. Thorell, 1881 : 493, 706. Simon, 1901 : 407. Roewer, 1954 : 934. Bonnet, 1956 : 1173. Prószyński, 1971 : 391. Wanless, 1981 : 256.

Diagnosis. From other species of *Cocalodes* by the long slender prongs of the median apophysis (Fig. 7H, I) in males, and the appearance of the epigyne (Figs 7C–F; 20A, B) in females.

Holotype female. In fair condition. *Carapace*: yellow-brown with pale yellowish eye region. *Eyes*: with black surrounds except AM; fringed in whitish hairs. *Clypeus*: densely white haired. *Chelicerae*: yellow-brown thinly clothed in testaceous hairs; pro- and retromargins with three teeth. *Maxillae*: yellow-brown with pale yellow blades. *Labium*: yellow-brown tipped yellow. *Sternum*: yellow-brown. *Abdomen*: long and tapered; pale yellow. *Legs*: generally yellow-brown; spines strong and numerous on legs I becoming weaker and fewer on posterior legs. Spination of legs I: metatarsi v 2–2–2, p 1–0–0, d 0–2–2, r 1–0–0; tibiae v 2–4–0, p 1–1–2, d 1–1–0, r 1–1–2; patellae p 1–0–0, r 1–0–0; femora p 1–0–1, d 1–1–3, r 0–1–0. *Epigyne* (Fig. 7D): somewhat translucent; the ducts will probably be less evident in freshly preserved specimens.

Dimensions (mm): total length c. 7·8; carapace length 2·88, breadth 2·34, height 1·72; abdomen length 4·88; eyes, anterior row 2·2, middle row 1·92, posterior row 2·0; quadrangle length 1·64 (56% of carapace length). *Ratios*: AM : AL : PM : PL :: 17 : 11 : 6 : 10; AL–PM–PL :: 9–12; AM : CL :: 17 : 3·5 (20% of AM diameter).

MALE (formerly undescribed) from Draeger Harbor, Papua New Guinea. In fair condition. *Carapace* (Fig. 7A, B): dark mahogany grading to orange-brown in eye region; irregularly clothed in short amber hairs (?rubbed) with white haired marginal band from level of coxae II to IV. *Eyes*: with black surrounds except AM; fringed by shining pale amber, and white hairs. *Clypeus*: fringed in light brownish hairs. *Chelicerae*: moderately elongate and porrect, more or less parallel; dark orange-brown, lighter distally; thinly clothed in fine light brownish hairs; teeth not examined; horn not evident. *Maxillae:* dark orange-brown with yellow-brown blades. *Labium*: dark orange-brown. *Sternum*: yellow-brown with amber margins, shiny; sparsely clothed in fine clear hairs. *Coxae*: coxae I yellow-brown below, dark mahogany above; other coxae yellow-brown. *Abdomen*: badly

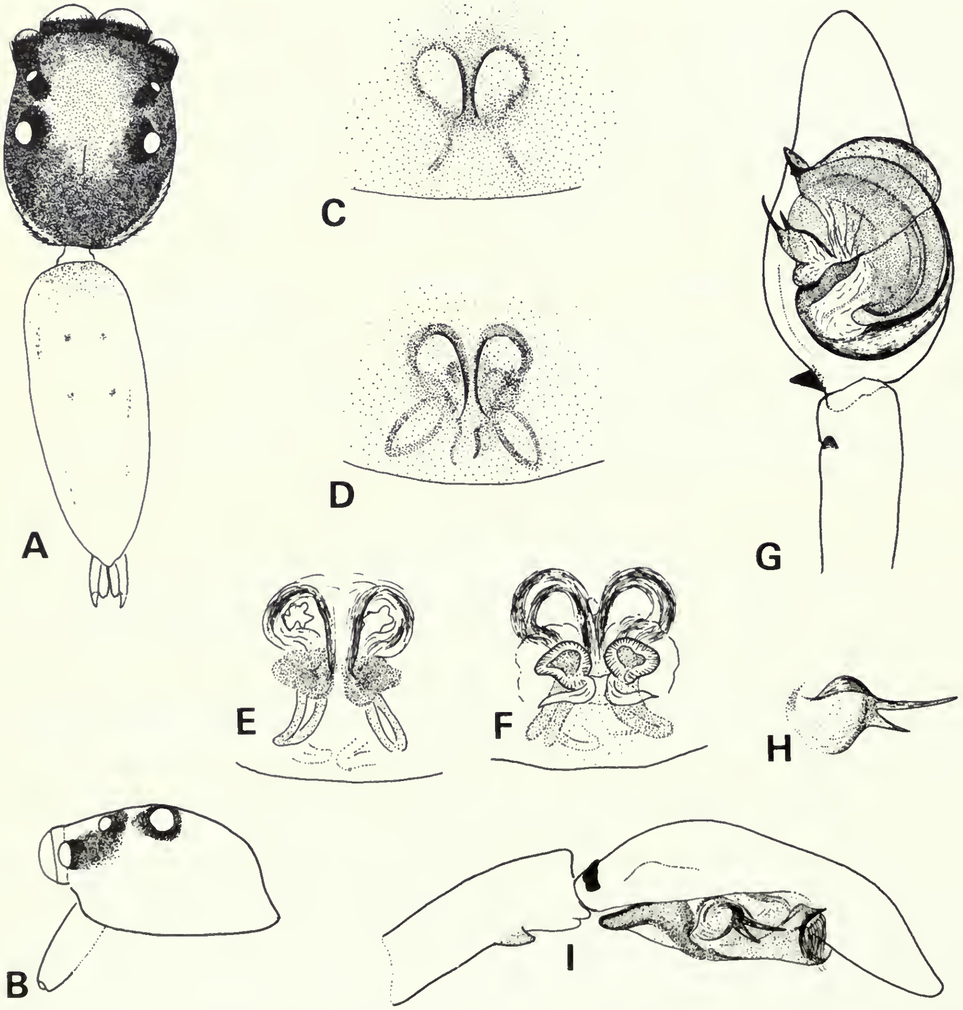

Fig. 7 *Cocalodes macellus* (Thorell). ♂: A, dorsal; B, carapace, lateral; G, palp, ventral; H, median apophysis; I, palp, retrolateral. Holotype ♀: D, epigyne. C, epigyne of another specimen; E, vulva, ventral; F, vulva, dorsal.

rubbed; yellow-brown with a dark patch anteriorly and ventral grey longitudinal band. *Legs*: legs I with tarsi and patellae yellow-brown, metatarsi yellow-brown suffused with black distally, tibiae dark mahogany with apices yellow-brown, femora dark mahogany; legs II–III yellow-brown; legs IV missing; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–0, d 1–2–2, r 1–0–0; tibiae v 3–2–4, p 0–1–1, d 1–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–2–2. *Palp* (Fig. 7G–I): femora brown-black with distal third light yellow, other segments light yellow; both prongs of median apophysis relatively long and slender.

Dimensions (mm): total length 5·68; carapace length 2·32, breadth 1·92, height 1·48; abdomen length 3·2; eyes, anterior row 1·85, middle row 1·56, posterior row 1·72; quadrangle length 1·4 (60% of carapace length). *Ratios*: AM : AL : PM : PL :: 15 : 9 : 4 : 8·5; AL–PM–PL :: 9·5–10; AM : CL :: 15 : 4·5 (30% of AM diameter).

VARIATION. ♀ from Papua New Guinea measures c. 6·9 mm total length, 2·76 mm carapace length.

The epigyne (Fig. 7C) is slightly less translucent and the looped ducts are less conspicuous.

DISTRIBUTION. Indonesia: Amboina; Papua New Guinea.

MATERIAL EXAMINED. **Amboina**: holotype ♀, juvenile, (*O. Beccari*) (MCSN, Genova). **Papua New Guinea**: Draeger Harbour, 5 miles E. of Finschhafen, 1♀, vi.1944 (*G. H. Penn*) (AMNH, New York); Nr. River Song, 6 miles W. of Finschhafen, 1♂, viii-ix. 1944, (*T. F. Delaney*) (AMNH, New York).

Cocalodes longicornis sp. n.

(Figs 8A–H; 21A)

DIAGNOSIS. From males of *C. longipes* and *C. innotabilis* by the absence of peg-like cymbial spines, and from male *C. platnicki* by the thickened dorsal prong of the median apophysis (Fig. 8B, C). Females, presumed to be of this species, most closely resemble females of *C. macellus*, but may be separated by the lack of a dense covering of white hairs on the clypeus and by the laterally extended introductory ducts (Figs 8F, G, H; 21A) of the epigynum.

MALE HOLOTYPE. In fair condition. *Carapace* (Fig. 8A, D): dark rufose with eye region dark amber; sparsely clothed in short fine amber hairs with whitish hairs in foveal region and a narrow marginal band of white hairs extending from level of coxae II to IV. *Eyes*: with black surrounds except AM; fringed by shining amber hairs with white hairs outside AL's. *Clypeus*: densely white haired below AM, sparsely amber haired below AL. *Chelicerae*: elongate, porrect and diverging; rufose; shiny; pro- and retro-margins evidently with three teeth; horn well developed and protruding well beyond clypeal margin. *Maxillae*: orange-brown grading to yellow-brown along inner margins. *Labium*: orange-brown. *Sternum*: orange-brown with darker margins; sparsely clothed in coarse black hairs marginally with fine pale brown hairs centrally. *Coxae*: orange-brown. *Abdomen*: dull orange-brown with blackish lateral bands above and central blackish band below; spinnerets orange-brown. *Legs*: legs I–II dark rufose with orange-brown tarsi, other legs rufose grading to orange-brown distally; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–1, d 0–1–0, r 1–0–1; tibiae v 2–2–2, p 1–1–1, d 1–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora r 1–1–1, d 0–2–3, p 1–1–1. *Palp* (Fig. 8B, C, E).

Dimensions (mm): total length 10·16; carapace length 4·28, breadth 3·5, height 2·64; abdomen length 5·84; eyes, anterior row 2·84, middle row 2·48, posterior row 2·5; quadrangle length 2·12 (49% of carapace length). *Ratios*: AM : AL : PM : PL :: 21 : 13·5 : 8 : 13; AL–PM–PL :: 12–18; AM : CL :: 21 : 7·5 (35% of AM diameter).

FEMALE PARATYPE. In fair condition. *Carapace*: orange-brown with reddish brown eye region and dark red-brown markings from PL's to thoracic margin; clothed in fine shining hairs (mostly rubbed). *Eyes*: with black surrounds except AM; fringed by whitish and pale amber hairs. *Clypeus*: fringed in whitish hairs. *Chelicerae*: robust, inclined anteriorly and slightly diverging; reddish with darker markings; shiny; sparsely fringed in pale amber hairs; pro- and retromargins with three teeth. *Maxillae and labium*: amber. *Sternum*: amber with darker margins; shiny; thinly clothed in fine light amber hairs. *Abdomen*: long and tapered; dull yellow-brown with blackish lateral markings; spinnerets yellow-brown. *Legs*: legs I amber with darker metatarsi; other legs amber to pale amber with black spots on femora IV; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–1, d 0–1–1, r 1–0–1; tibiae v 3–2–2, p 0–1–1, d 0–1–0, r 1–1–1; patellae p 1–0–0,

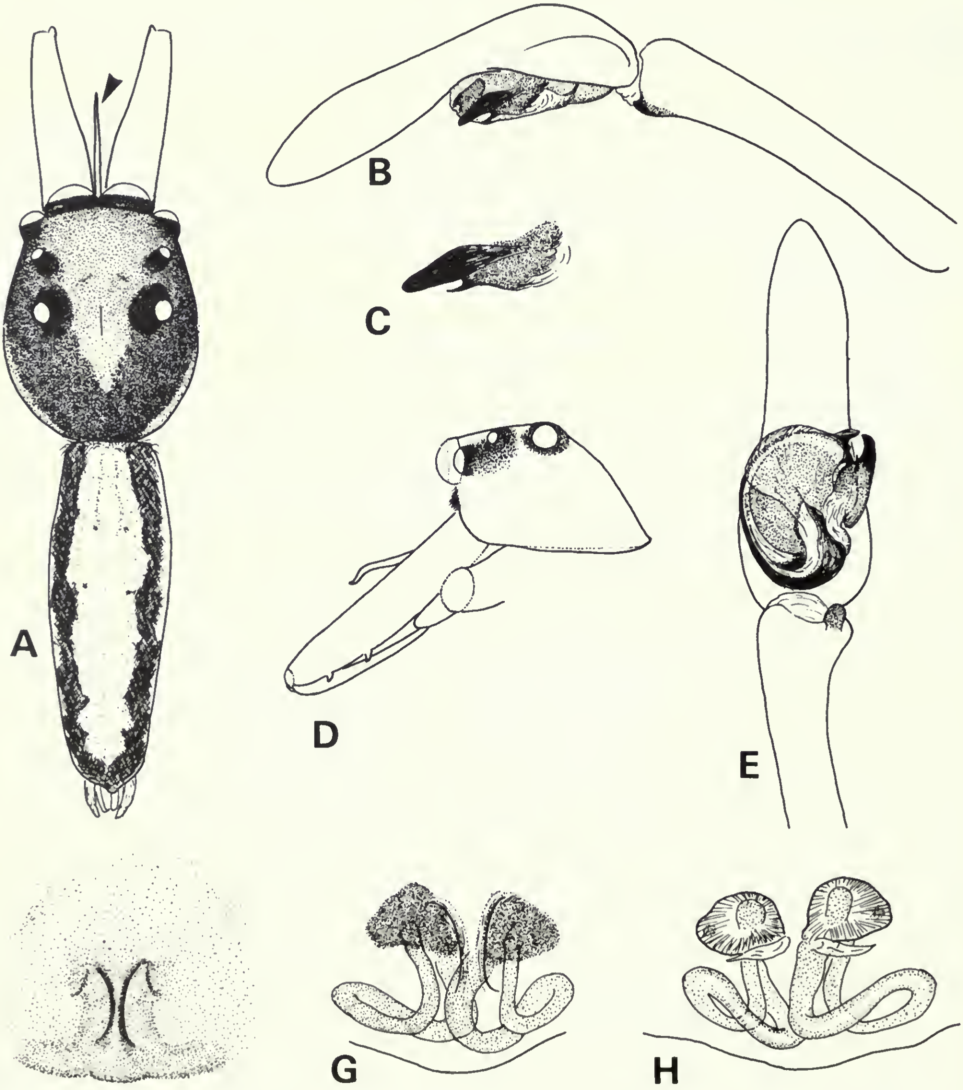

Fig. 8 *Cocalodes longicornis* sp. n. Holotype ♂: A, dorsal; B, palp, retrolateral; C, median apophysis; D, carapace and chelicera, lateral; E, palp, ventral. Paratype ♀: F, epigyne; G, vulva, ventral; H, vulva dorsal.

r 1–0–0; femora p 1–1–1, d 0–2–3, r 0–1–0. *Epigyne* (Fig. 8F–H; 21A): relatively simple, the openings lead into narrow introductory ducts which extend and loop laterally before joining the spermathecae.

Dimensions (mm): total length c. 6·4; carapace length 3·32, breadth 2·88, height 2·08; abdomen length c. 3·0; eyes, anterior row 2·6, middle row 2·32, posterior row 2·44; quadrangle length 2·0 (60% of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 12 : 7 : 12; AL–PM–PL :: 13 : 15·5; AM : CL :: 19 : 5 (26% of AM diameter).

VARIATION. ♂ total length varies from 10·0 to 10·16 mm, carapace length 3·76–4·16 mm (three specimens). Another ♀ measures c. 8·0 mm total length, 3·0 mm carapace length.

DISTRIBUTION. Papua New Guinea.

MATERIAL EXAMINED. **Papua New Guinea**: D'Entrecasteaux Islands, Normanby Island, Mt. Pabinama, about 3 miles ENE of Cape Prevost, 820 m, camp 2, 1956 (*J. L. Brass*, 5th Archbold Exp., to New Guinea) holotype ♂, (AMNH, New York), paratype ♂ (BMNH. 1981.2.2.1); Fergusson Island, Agamoia about 3 miles S. of Lake Ruaba, 200 m, camp 5, 18–24. vi.1956 (J. L. Brass, 5th Archbold Exp., to New Guinea) paratype ♂, paratype ♀, (AMNH, New York); New Britain, Ralum, (nr. Kokopo) Lowan, on tree trunk, paratype ♀, 27.xii.1896 (*F. Dahl*) (MNHU, Berlin. 17799).

Cocalodes protervus (Thorell)
(Fig. 9A–B)

Cocalus protervus Thorell, 1881 : 493, ♀. Holotype ♀, West Irian (MCSN, Genova) [examined]. Simon, 1901 : 407. Roewer, 1954 : 935. Bonnet, 1956 : 1174. Prószyński, 1971 : 391. Wanless 1981 : 256.

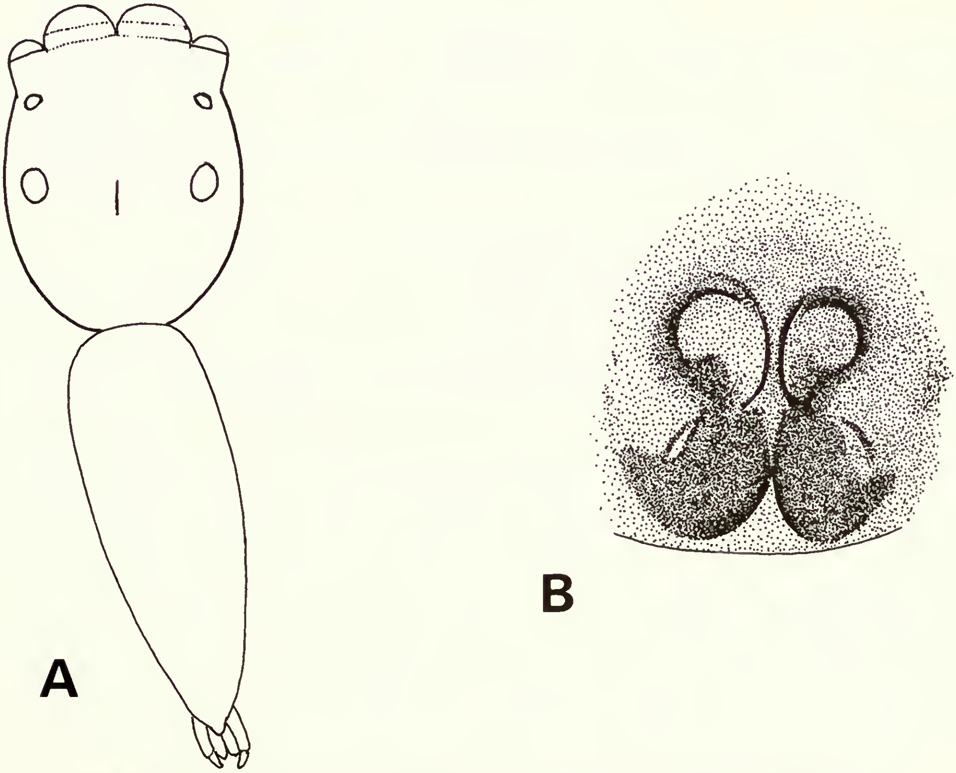

Fig. 9 *Cocalodes protervus* (Thorell). Holotype ♀: A, dorsal; B, epigyne.

DIAGNOSIS. Similar to *C. macellus* and *C. longicornis* from which it differs by the large darkened spermathecae (Fig. 9B).

MALE. Unknown.

FEMALE HOLOTYPE. In poor condition. *Carapace* (Fig. 9A): brownish with scattered white hairs, rubbed. *Eyes*: with black surrounds except AM; fringed by whitish hairs. *Clypeus*: densely white haired. *Chelicerae*: robust, inclined anteriorly and slightly diverging; brownish with sooty markings; sparsely clothed in light brown hairs; pro- and retromargins with three teeth. *Maxillae and labium*: pale brown. *Sternum*: pale brown with darker margins. *Coxae*: generally brownish. *Abdomen:* greyish yellow with darker somewhat mottled longitudinal lateral markings; clothed in short recumbent amber hairs. *Legs*: dark brown; spines long, slender and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–2–1, d 1–0–0, r 1–0–1; tibiae v 4–3–3, p 0–2–1, d 1–1–0, r 0–0–1; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–2–3, r 0–2–0. *Epigyne* (Fig. 9B): rather dark, openings separated by distinct septum with black disc-like spermathecae posteriorly.

Dimensions (mm): total length 6·8; carapace length 3·04, breadth 2·46, height 1·84; abdomen length 3·84; eyes, anterior row 2·32, middle row 1·98, posterior row 2·08; quadrangle length 1·72 (56% of carapace length). *Ratios*: AM : AL : PM : PL :: 18 : 11 : 6 : 10; AL–PM–PL :: 11–13; AM : CL :: 18 : c. 7 (c. 38% of AM diameter).

DISTRIBUTION. West Irian.

MATERIAL EXAMINED. **West Irian**: Pulo Faor, holotype ♂, 1872, (*L. M. D'Albertis*) (MCSN, Genova).

Cocalodes thoracicus Szombathy
(Figs 10A–E; 11A–E; 18D; 20C, D)

Cocalodes thoracicus Szombathy, 1915 : 470, ♂, ♀. Syntypes, Papua New Guinea (?in Természettudományi Múzeum, Budapest) [not examined]. Roewer, 1954 : 936. Bonnet, 1956 : 1173.

REMARKS. Although it was not possible to examine the type specimens of *C. thoracicus* it may be recognized with a fair degree of confidence from Szombathy's original figures, which show the distal cheliceral lobes (arrowed, Fig. 10A) to be more pronounced in this species than in others of the genus.

DIAGNOSIS. From other species of *Cocalodes* by the more or less equal development of the prongs of the median apophysis (Figs 10C, D; 18D) in males, and by the relatively broad epigynal septum (Fig. 11B, C) in females.

MALE from Morobe Province. In good condition, but legs detached. *Carapace* brown-black with dark orange-brown eye area and central yellow-brown stripe from foveal region to posterior margin; clothed dorsally in fine shining pale amber and whitish hairs with short coarse black hairs around thoracic margins. *Eyes*: with black surrounds except AM; fringed by pale amber and whitish hairs. *Clypeus*: sparsely covered in pale amber and blackish hairs. *Chelicerae*: elongate and porrect with distal lobes; black with bluish metallic sheen under some angles of illumination; proximally sparsely clothed in stiff black hairs; promargin with four teeth, retromargin with two; horn protruding just beyond clypeal margin. *Maxillae*: brownish black grading to yellow-brown distally. *Labium*: brown-black tipped yellow-brown. *Sternum*: yellow-brown faintly tinged black with brownish orange margins. *Coxae*: pale yellow. *Abdomen*: with four impressed spots; mottled grey-black with a dorsal greyish yellow band having vague sooty markings; ventrally a longitudinal black stripe; irregularly clothed in minute setae with scattered long blackish hairs; spinnerets mottled yellow-brown and black. *Legs*: legs I tarsi pale yellow, metatarsi black with pale yellow basal region, tibiae black distally grading to dark yellow-brown to black proximally, patellae black distally grading to yellow-brown proximally,

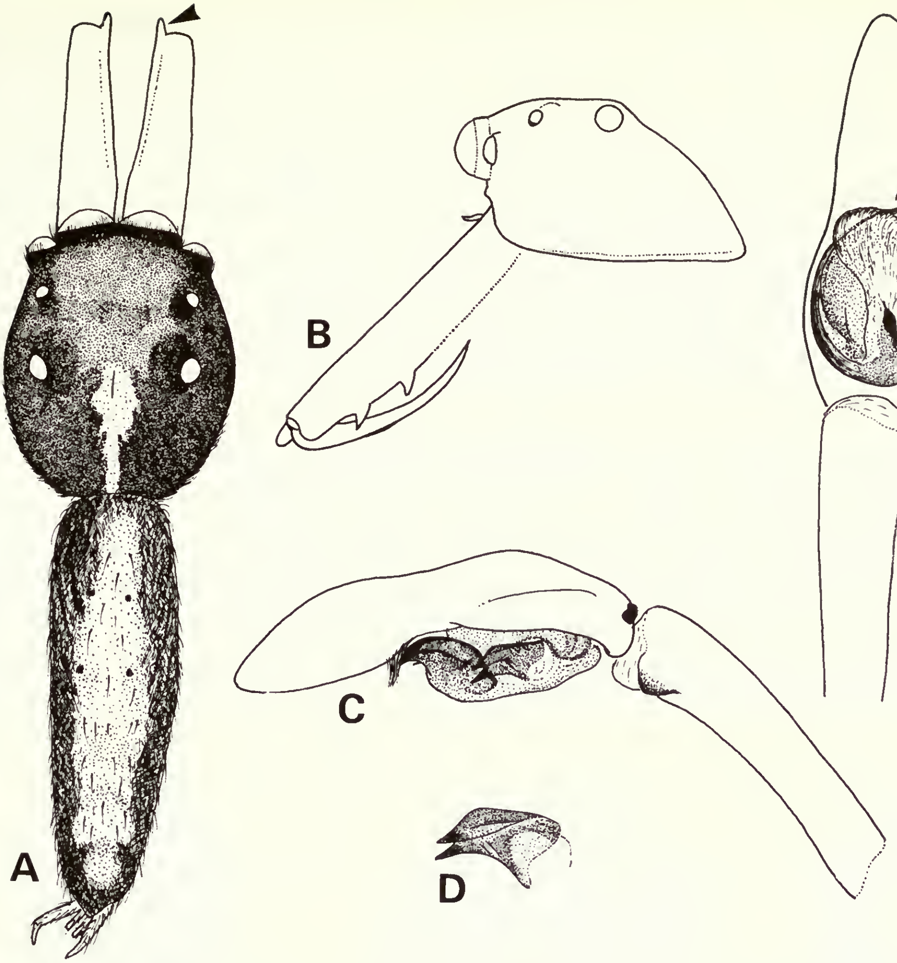

Fig. 10 *Cocalodes thoracicus* Szombathy. ♂: A, dorsal; B, carapace, lateral; C, palp, retrolateral; D, median apophysis; E, palp, ventral.

femora yellow to yellow-brown; legs II as I, but tibiae and patellae yellow-brown; legs III yellow-brown to pale yellow-brown; legs IV similar, but with vague darker markings; spines strong and numerous. Spination of legs I: matatarsi v 2–2–2, p 1–0–0, r 1–0–1; tibiae v 2–2–2, p 1–1–1, d 1–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 1–1–2, d 0–2–1, r 0–1–2. *Palp* (Figs 10C–E; 18D).

Dimensions (mm): total length 9·28; carapace length 3·48, breadth 3·16, height 2·28; abdomen length 5·36; eyes, anterior row 2·56, middle row 2·28, posterior row 2·37; quadrangle length 2·08 (59% of carapace length). *Ratios*: AM : AL : PM : PL :: 20 : 12 : 8 : 12; AL–PM–PL :: 13–15·5; AM : CL :: 20 : 5 (25% of AM diameter).

FEMALE from Madang Province. In good condition. *Carapace* (Fig. 11A): yellow-brown with orange-brown eye region, a thin dark brown border line, lateral brownish stripes and dark brown bands from PL's to thoracic margin; clothed in very fine shining amber and whitish hairs. *Eyes*: with black surrounds except AM; fringed in shining pale amber and whitish hairs. *Clypeus*: sparsely covered in white hairs. *Chelicerae*: robust, inclined anteriorly and diverging; yellow-brown; shiny; thinly clothed in testaceous hairs; promargin with four teeth, retromargin with three. *Maxillae and labium*: pale yellow-brown. *Sternum*: pale yellow-brown with darker margins; sparsely clothed in testaceous hairs. *Coxae*: pale yellow-brown. *Abdomen*: similar to ♂ except for pale yellow venter and covering of dark amber hairs over lateral bands. *Legs*: legs I yellow-brown with darker markings and a black streak on inside of femora; legs II yellow-brown with brownish markings; legs III yellow-brown; legs IV yellow-brown with brownish markings and black spots on femora and patellae; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–1, r 1–0–1; tibiae v 2–2–2, p 1–1–2, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 0–2–2, d 0–2–1, r 0–2–0. *Epigyne* (Figs 11B–E; 20C, D): relatively simple, but variable; the obscure openings (arrowed, Fig. 11D) lead into wide ducts which narrow and loop posteriorly before entering the spermathecae.

Dimensions (mm): total length 9·28; carapace length 3·32, breadth 2·84, height 1·96; abdomen length 5·6; eyes, anterior row 2·44, middle row 2·2, posterior row 2·28; quadrangle length 1·92 (57% of carapace length). *Ratios*: AM : AL: PM : PL :: 18 : 12 : 7 : 11; AL–PM–PL :: 12·5–15; AM : CL :: 18 : 5 (27 per cent of AM diameter).

VARIATION. ♂ total length varies from 6·9 to 11·5 mm, carapace length 2·72–4·4 mm (14 specimens). ♀ total length 7·28–10·8 mm, carapace length 2·84–4·08 mm (nine specimens).

The cheliceral horn, possibly an allometric growth character, only protrudes well beyond the clypeus in large specimens. The epigynal septum varies from rectangular to triangular in outline (Fig. 11B, C) and the rod-like extensions of the spermathecae (in reality part of the introductory ducts), are not always evident in uncleared epigynes.

DISTRIBUTION. Papua New Guinea; Irian Jaya.

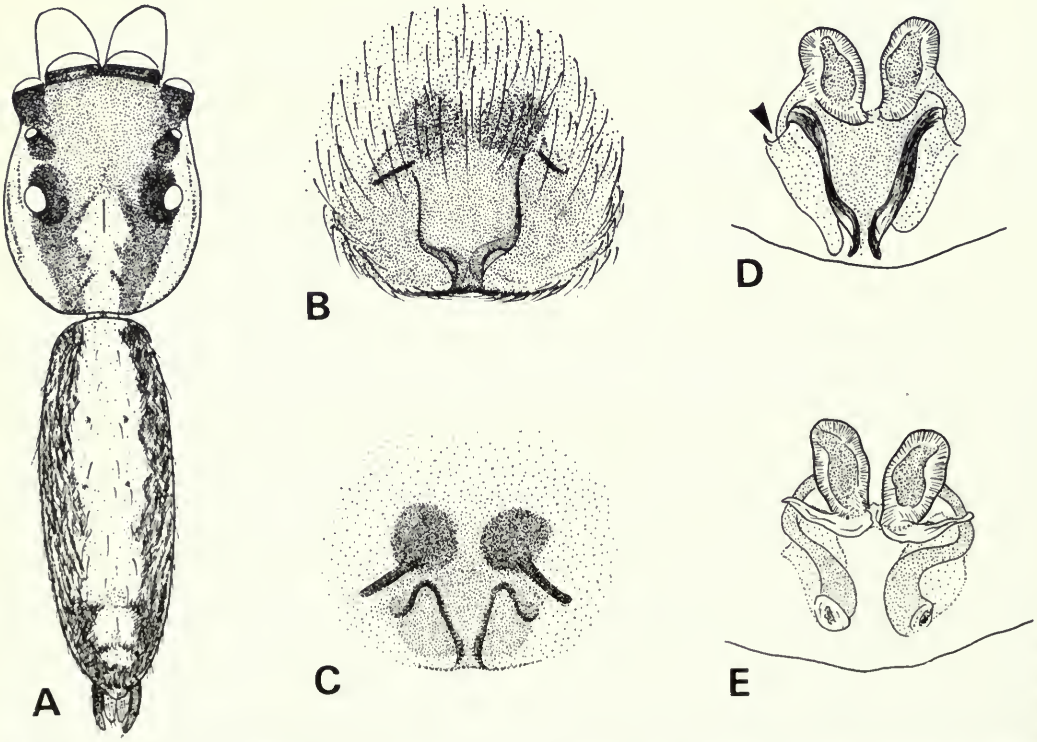

Fig. 11 *Cocalodes thoracicus* Szombathy. ♀: A, dorsal; B, epigyne: C, epigyne of another specimen; D, vulva, ventral; E, vulva, dorsal.

MATERIAL EXAMINED. **Papua New Guinea**: Morobe Province, Wau: 1♀, iv.1979 (*H. W. Levi*); 1♀, iv.1979 (*M. Robinson*); 1♀, iv.1979, beating vegetation in forest, (*H. W. Levi*); 3♂♂, 1♀, McAdam Park, 4.iv.1979 (*H. W. Levi, Y. Lubin, M. Robinson*); Madang Province, 25 Km, N. of Madang, teak forest, night collection, 1♂, 21.iii.1979 (*H. W. Levi, Y. Lubin. B. Robinson*) (MCZ. Harvard); Draeger Harbour: 5 miles E. of Finschhafen, 1♂, vi.1944 (*G. H. Penn*) (AMNH, New York); Maffin Bay: 1♂, xii.1944 (Lt. *Geo. B. Sirotiak*) (AMNH. New York); Astrolabe Bay, 1♀, (*R. Rohde*) (MNHN, Berlin. 17794); Ramu, 1♂, (*F. Dahl,* Ramu Expedition) (MNHN, Berlin. 17801); Jagei River, 1♂, 2.viii.1896 (*Lauterbach*) (MNHN, Berlin, 17796). **Irian Jaya**: Sukarnapura (Hollandia): 2♂♂, 5.i.1945 (*L. W. Saylor*); 1♂, iv.1945 (*Borys Malkin*); 1♂, 14.v.1945 *Borys Malkin*); rain forest, 250 ft. 2♂♂, xii.1944 (*H. Hoogstraal*) (AMNH, New York); Humboldts Bay, 200 ft. 1♀, iv.1936 (*L. E. Cheesman*) (BMNH. 1937.12.13.425); Cyclops Mts. Sabron, 2,200 ft. 1♀, v.1936 (*L. E. Cheesman*) (BMNH. 1937.12.13.541).

Cocalodes turgidus sp. n.

(Figs 12A–D; 20E, F)

DIAGNOSIS. Like *C. thoracicus*, but differs by the median swelling of the epigynal septum (Fig. 12B).

MALE. Unknown.

FEMALE HOLOTYPE. In fair condition. *Carapace* (Fig. 12A): yellow-brown with orange-brown eye region, dark brown lateral margins and dark brown stripes below the lateral eyes to posterior margin; clothed in minute creamy white setae with light brownish hairs around thoracic margins. *Eyes*: with black surrounds except AM; irregularly fringed by creamy

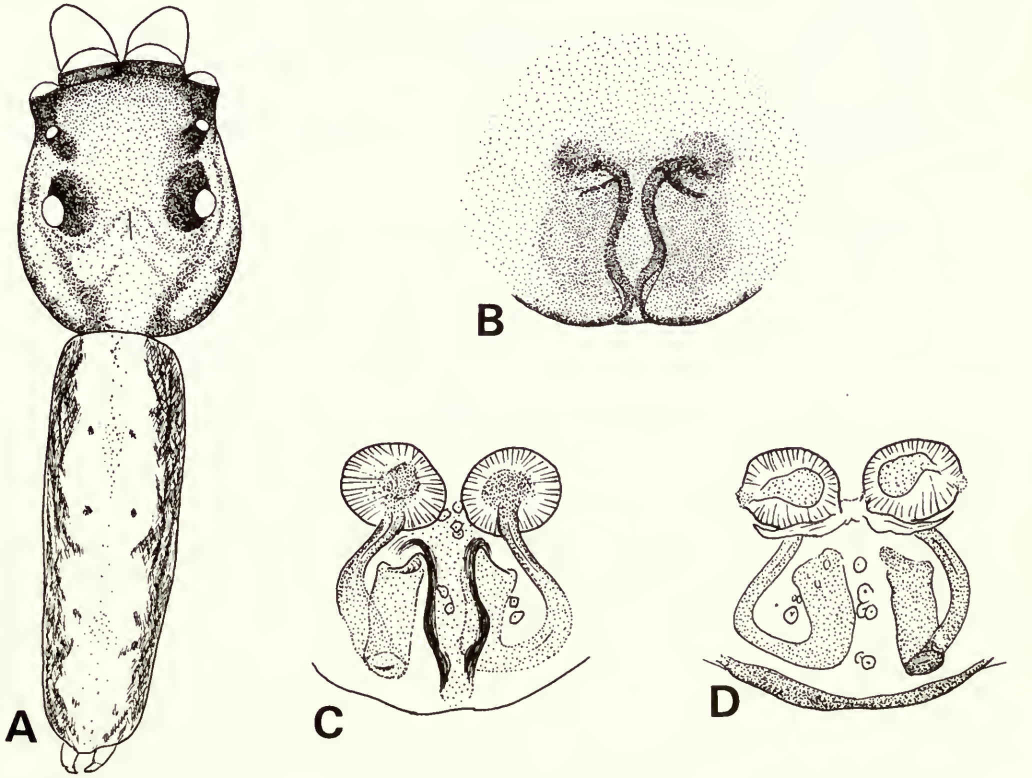

Fig. 12 *Cocalodes turgidus* sp. n. Holotype ♀: A, dorsal; B, epigyne. Paratype ♀: C, vulva, ventral; D, vulva, dorsal.

white hairs. *Chelicerae*: robust, inclined anteriorly and diverging; amber with brownish markings; shiny; thinly clothed in clear pale amber hairs; pro- and retromargins with three teeth. *Maxillae*: yellow-brown with inner distal margins whitish yellow. *Labium*: yellow-brown. *Sternum*: light yellow-brown with darker margins; shiny; thinly clothed in testaceous hairs. *Coxae*: pale yellow-brown. *Abdomen*: with four impressed spots; pale yellow with black lateral stripes and a black ventral band. *Legs*: legs I with tarsi yellow-brown, metatarsi blackish grading to light orange-brown proximally, tibiae yellow-brown with blackish annuli, patellae yellow-brown, femora yellow-brown with blackish streaks; other legs similar, but darker markings less extensive especially on legs III–IV; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–0, d 0–1–0, r 1–0–1; tibiae v 2–2–2, p 0–1–1, d 0–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 1–1–0, d 0–2–3, r 0–1–1. *Epigyne* (Figs 12B–D; 20E, F).

Dimensions (mm): total length 8·72; carapace length 3·32, breadth 2·88, height 1·96; abdomen length 5·28; eyes, anterior row 2·44, middle row 2·18, posterior row 2·32; quadrangle length 2·02 (60% of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 12 : 8 : 12; AL–PM–PL :: 11–16; AM : CL :: 19 : 5 (26% of AM diameter).

VARIATION. A paratype ♀ measures 8·64 mm total length, 3·28 mm carapace length.

DISTRIBUTION. Irian Jaya.

MATERIAL EXAMINED. **Irian Jaya**: Sansapor, holotype ♀, paratype ♀, viii–ix.1944 (*R. B. Burrows*, A.P.O. 159) (AMNH, New York).

Cocalodes longipes (Thorell)
(Fig. 13A–G)

Cocalus longipes Thorell, 1881 : 494, 707, ♀, ♂. LECTOTYPE ♀, Yule Isl. PARALECTOTYPE ♂, Ceram Isl. (here designated) (MCSN, Genova) [examined]. Simon, 1901 : 407. Roewer, 1954 : 935. Bonnet, 1956 : 1173. Prószyński, 1971 : 391. Wanless 1981 : 256

DIAGNOSIS. From other species of *Cocalodes* by the scimitar-shaped dorsal prong of the median apophysis (Fig. 13E) in males, and by the comma-like introductory ducts (Fig. 13B) in females.

FEMALE LECTOTYPE. In fair condition. *Carapace* (Fig. 13D, F): orange-brown with sooty markings; irregularly clothed in short recumbent white hairs. *Eyes*: with black surrounds except AM; fringed by whitish hairs. *Clypeus*: thinly clothed in fine whitish hairs. *Chelicerae*: robust, inclined anteriorly and slightly diverging; dark amber; thinly clothed in white and light amber hairs; pro- and retromargins with three teeth. *Maxillae*: orange-brown with lighter inner margins. *Labium*: orange-brown. *Sternum*: amber with darker margins. *Coxae*: generally yellowish orange to amber. *Abdomen*: pale yellow-orange with faint sooty lateral markings outlining a central pale band; spinnerets pale yellow-brown. *Legs*: brownish amber grading to light amber distally; spines numerous and robust. Spination of legs I: metatarsi v 2–1–1, p 1–1–1, d 0–0–2, r 1–0–0; tibiae v 4–4–2, p 0–1–1, d 0–1–0; patellae r 1–0–0, p 1–0–0; femora p 1–0–1, d 0–2–3, r 0–1–1. *Epigyne* (Fig. 13B): similar to *platnicki* and *signatus*, but readily separated by the comma-like ducts.

Dimensions (mm): total length c. 10·0; carapace length 3·76, breadth 3·32, height 2·36; abdomen length 5·92; eyes, anterior row 2·6, middle row 2·36, posterior row 2·41; quadrangle length 2·04 (54% of carapace length). *Ratios*: AM : AL : PM : PL ::20 : 12 : 7·5 : 12; AL–PM–PL :: 11·5–17; AM : CL :: 20 : 5 (25% of AM diameter).

MALE PARALECTOTYPE. In fair condition. *Carapace* (Fig. 13A): amber with vague brownish markings; rubbed. *Eyes*: with black surrounds except AM; irregularly fringed by creamy white hairs. *Clypeus*: fringed in greyish white hairs. *Chelicerae*: elongate, porrect and diverging distally; amber, shiny; very sparsely clothed in light amber hairs; pro- and retromargins with three teeth. *Maxillae and labium*: yellow-brown. *Sternum*: pale yellow-brown with darker margins. *Coxae*: yellow-brown. *Abdomen*: yellow-brown with

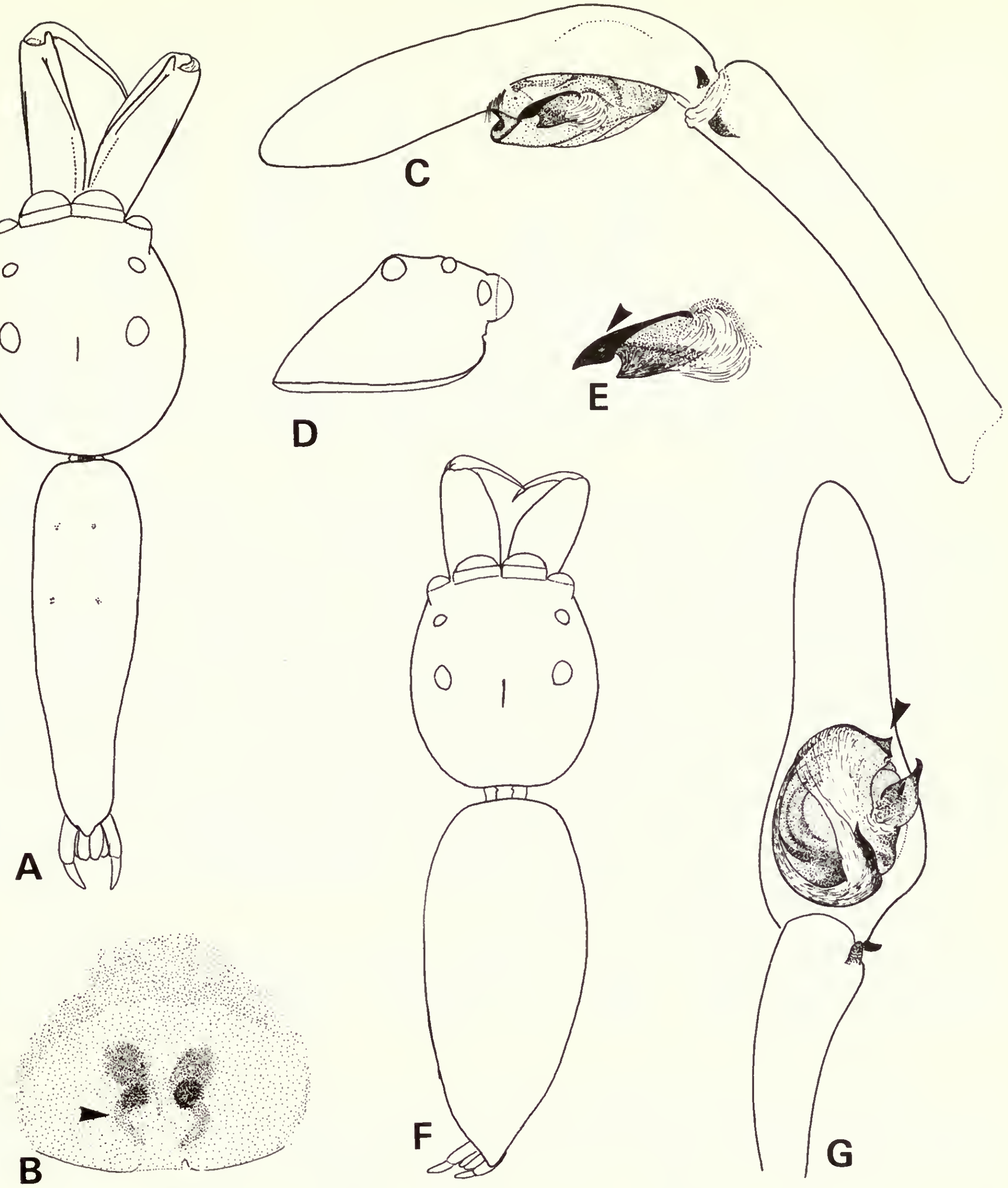

Fig. 13 *Cocalodes longipes* (Thorell). Paralectotype ♂: A, dorsal; C, palp, retrolateral; E, median apophysis; G, palp, ventral. Lectotype ♀: B, epigyne; D, carapace, lateral; F, dorsal.

faint sooty lateral markings; spinnerets yellow-brown. *Legs*: generally orange-brown; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–1–1, r 1–0–1; tibiae v 4–4–0, p 0–1–1, d 0–1–0, 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 1–1–1, d 0–2–3, r 0–2–0. *Palp* (Fig. 13C, E, G): the triangular tip of the functional conductor is distinctive.

Dimensions (mm): total length c. 9·9; carapace length c. 4·28, breadth 3·64, height 2·52; abdomen length 6·24; eyes, anterior row 2·88, middle row 2·55, posterior row 2·68; quadrangle length 2·32 (54% of carapace length). *Ratios*: AM : AL : PM : PL :: 22·5 : 14 : 8.5 : 14:5; AL–PM–PL :: 13–17; AM : CL :: 22·5 : 8 (35% of AM diameter).

DISTRIBUTION. Indonesia: Ceram Island; Papua New Guinea: Yule Island.

MATERIAL EXAMINED. **Indonesia**, Wahai, Ceram Island, paralectotype ♂, 1872, (*L. M. D'Albertis*). **Papua New Guinea**, Yule Island (*Roro*), lectotype ♀, 1872 (*L. M. D'Albertis*) (MCSN, Genova).

REMARKS. To judge from the geographical distribution, the male and female described above may not be conspecific.

Cocalodes platnicki sp. n.
(Figs 14A–J; 21C–F)

DIAGNOSIS. From other species of *Cocalodes* by the combined absence of peg-like cymbial spines and curved tip of the functional conductor (Fig. 14F) in males. Females are readily separated by the absence of an epigynal septum and broad posterior ledge (Fig. 14H).

MALE HOLOTYPE. In fair condition. *Carapace* (Fig. 14B, C): yellow-brown with dark brownish sides and thin yellow-brown border line; pale areas including border line clothed in short whitish hairs, elsewhere covered in short blackish hairs. *Eyes*: with black surrounds except AM; fringed by whitish hairs. *Clypeus*: fringed in long white hairs. *Chelicerae*: moderately elongate, robust, inclined anteriorly and slightly divergent; pale orange-brown; sparsely fringed by long white hairs along outer basal margin; pro- and retromargins with three teeth. *Maxillae and labium*: yellow-brown. *Sternum* (Fig. 14G): yellow-brown with darker margins; shiny. *Coxae*: yellow-brown; shiny. *Abdomen*: with two pairs of impressed spots: pale yellow with blackish lateral bands; spinnerets pale yellow-brown tinged black. *Legs*: legs I amber grading to pale yellow-brown distally with blackish markings on femora, distal half of tibiae and metatarsi; legs II similar to I, but markings less distinct; legs III–IV yellow-brown with vague sooty annuli on metatarsi and darkening towards apices of tibiae; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–1–1, r 1–0–1; tibiae v 2–2–2, p 1–1–2, d 0–0–1, r 1–1–2; patellae p 1–0–0, r 1–0–0; femora p 2–1–2, d 0–3–2, r 1–2–2. *Palp* (Fig. 14D–F).

Dimensions (mm): total length 7·2; carapace length 2·98, breadth 2·48, height 1·76; abdomen length 4·24; eyes, anterior row 2·28, middle row 2·02, posterior row 2·12; quadrangle length 1·8 (60% of carapace length). *Ratios*: AM : AL : PM : PL :: 18 : 11 : 7 : 11·5; AL–PM–PL :: 10–14; AM : CL :: 18 : 4 (22% of AM diameter).

FEMALE PARATYPE. In good condition. *Carapace* (Fig. 14A): dark orange-brown with yellow-brown markings; dark areas clothed in short blackish hairs with whitish hairs elsewhere. *Eyes*: more or less as in ♂. *Clypeus*: fringed by white hairs. *Chelicerae*: robust and moderately porrect; amber; sparsely clothed in whitish and pale amber hairs; pro- and retro-margins with three teeth. *Maxillae and labium*: pale yellow-brown. *Sternum*: pale yellow-brown; thinly covered in testaceous hairs. *Coxae*: pale yellow-brown. *Abdomen*: similar to ♂, but ventrally with a pale greyish band from epigyne to spinnerets. *Legs*: legs I–II yellow-brown with vague darker markings and blackish femoral stripes; other legs yellow-brown with sooty spots on femora, darkened tibial apices and sooty annuli of metatarsi; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–0, d 0–1–2, r 1–0–0; tibiae v 2–2–2, p 1–1–1, d 0–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 1–1–1, d 0–2–3, r 0–2–0. *Epigyne* (Figs 14H–J; 21C–F): only species in genus known to have secondary spermathecae.

Dimensions (mm): total length 8·96; carapace length 3·44, breadth 2·84, height 2·0; abdomen length 5·28; eyes, anterior row 2·52, middle row 2·18, posterior row 2·28; quadrangle length 2·0 (58% of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 12 : 8 : 12; AL–PM–PL :: 13–16·5; AM : CL :: 19 : 4 (21% of AM diameter).

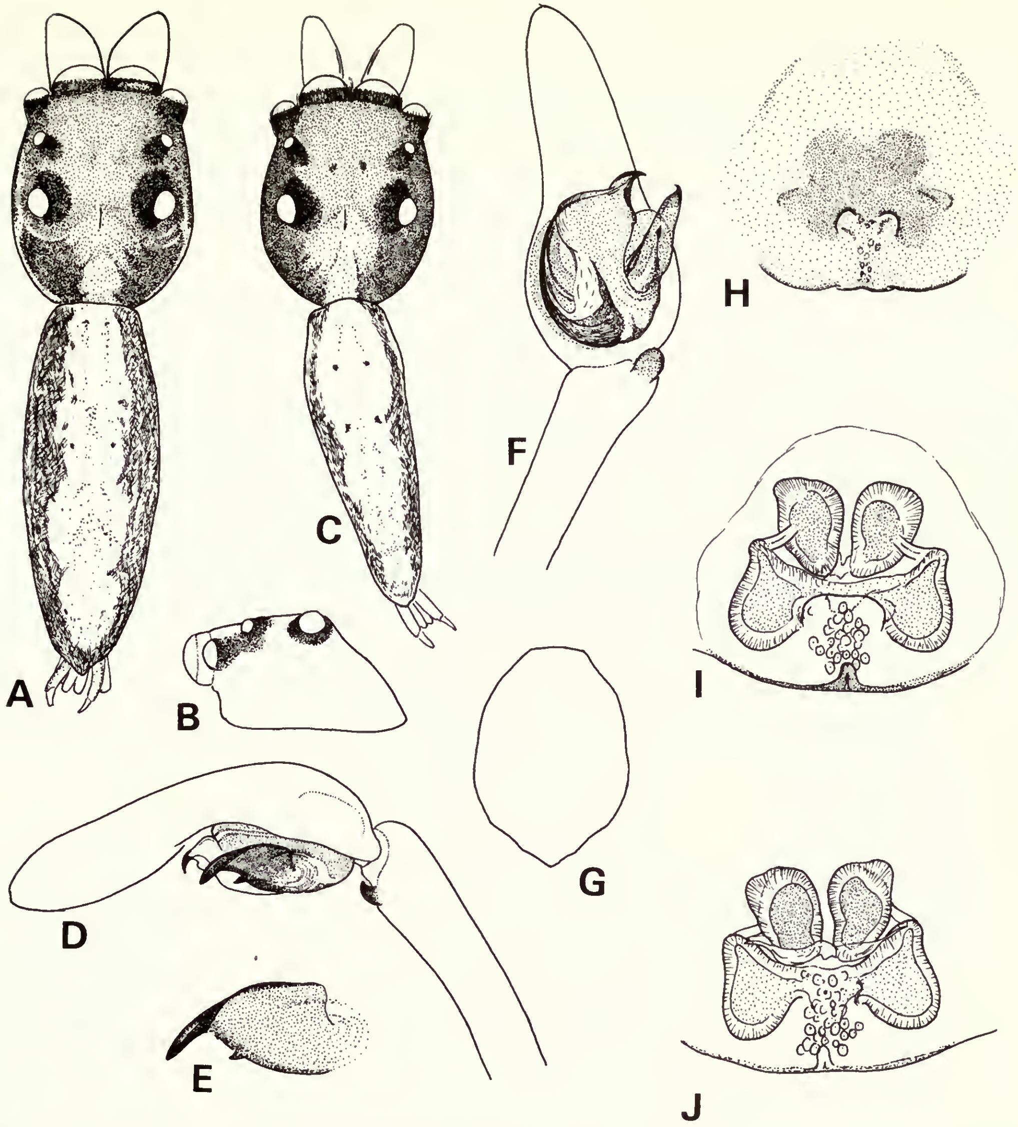

Fig. 14 *Cocalodes platnicki* sp. n. Holotype ♂: B, carapace, lateral; C, dorsal; D, palp, retrolateral; E, median apophysis; F, palp, ventral; G, sternum. Paratype ♀: A, dorsal; H, epigyne; I, vulva, dorsal; J, vulva, ventral.

VARIATION. Paratype ♂ measures 9·6 mm total length, 3·72 mm carapace length. Paratype ♀ c. 9·1 mm total length, 3·24 mm carapace length.

DISTRIBUTION. Irian Jaya.

MATERIAL EXAMINED. **Irian Jaya,** Sukarnapura (Hollandia): tropical rain forest, holotype ♂, paratype ♀, 31.xii.1944 (*L. W. Saylor*) (AMNH, New York); paratype ♀, 5.i.1945 (*L. W. Saylor*) (AMNH, New York); paratype ♂, rain forest, xii.1944, (*H. Hoogstraal*) (AMNH, New York).

ETYMOLOGY. This species is named after Dr N. I. Platnick, American Museum of Natural History, New York.

Cocalodes innotabilis sp. n.
(Figs 15A–F; 18A, B)

Diagnosis. Similar to males of *C. longipes* and *C. longicornis*, but separated by the combined presence of peg-like cymbial spines and the finger-like dorsal prong of the median apophysis (Fig. 15D, E).

Female. Unknown. *C. expers* from Fergusson Island may belong here or possibly the female of *C. longipes*, from Yule Island (Papua New Guinea), which seems doubtfully matched with the male known only from Seram (Indonesia).

Male holotype. In fair condition. *Carapace* (Fig. 15A, B): orange-brown with dark reddish brown sides and light orange margins; weakly iridescent under some angles of illumination; rubbed. *Eyes*: with black surrounds except AM; fringed in whitish and pale amber hairs. *Clypeus*: sparsely fringed by fine pale brownish hairs. *Chelicerae*: moderately long, inclined anteriorly; dark reddish brown, weakly iridescent blue under some angles of illumination; thinly covered in stiff brownish hairs; pro- and retromargins with three teeth; horn moderately long, but not protruding beyond clypeus. *Maxillae*: orange-brown to light yellowish along inner and distal margins. *Labium*: orange-brown tipped light yellow. *Sternum*: pale amber with darker margins; shiny. *Coxae*: pale amber. *Abdomen*: with two pairs of impressed spots; yellow-brown with brownish lateral bands above and central blackish band below; rubbed; spinnerets light orange-brown tinged black. *Legs*: tarsi light amber, metatarsi dark brown with light brownish hairs grading to amber with

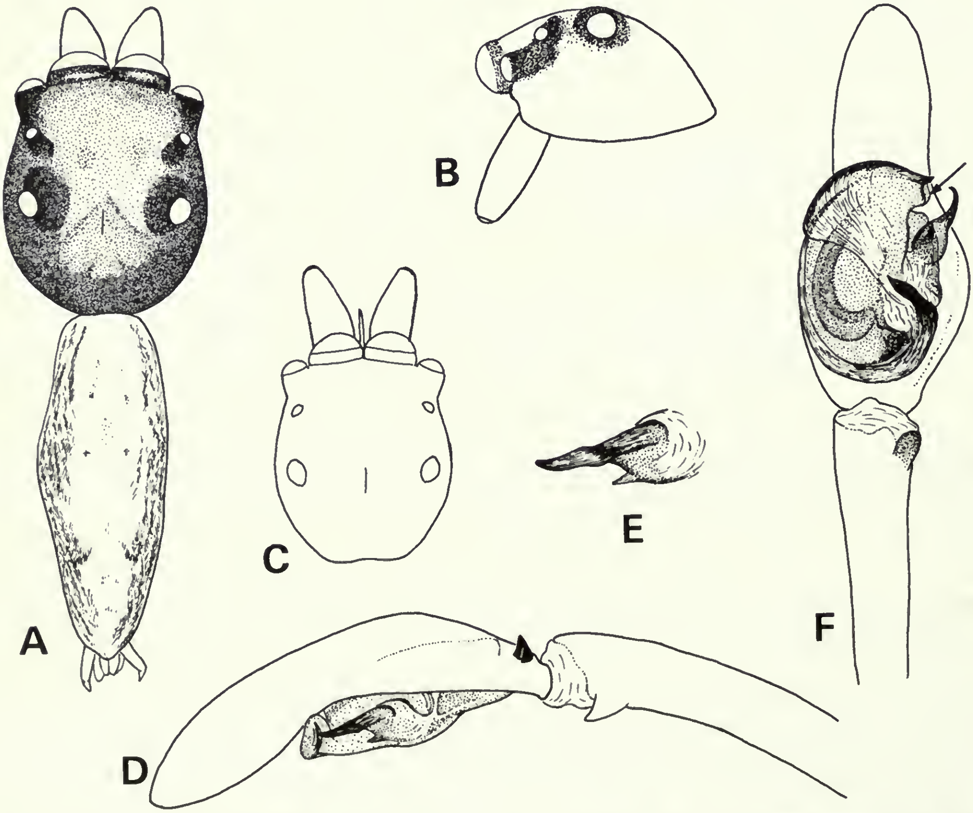

Fig. 15 *Cocalodes innotabilis* sp. n. Holotype ♂: dorsal; B, carapace, lateral; D, palp, retrolateral; E, median apophysis; F, palp, ventral. Paratype ♂: C, carapace, dorsal, showing cheliceral horn.

white hairs proximally, tibiae dark brown, patellae brownish grading to amber proximally, femora amber; other legs amber; spines strong and numerous. Spination of legs I: metatarsi v 2–2–2, p 1–0–0, d 0–1–2, r 1–0–1; tibiae v 2–2–2, p 1–1–1, d 1–1–0, r 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 1–1–1, d 0–2–3, r 0–1–1. *Palp* (Figs 15D–F; 18A, B); the lobe associated with the tip of the functional conductor (arrowed, Fig. 15F) is also characteristic of this species.

Dimensions (mm): total length 6·96; carapace length 2·88, breadth 2·4, height 1·84; abdomen length 4·0; eyes, anterior row 2·26, middle row 2·04, posterior row 2·18; quadrangle length 1·72 (59% of carapace length). *Ratios*: AM : AL : PM : PL :: 18 : 11 : 6 : 11; AL–PM–PL :: 10–13; AM : CL :: 18 : 5 (27% of AM diameter).

VARIATION. ♂ total length varies from 5·9 to 8·2 mm, carapace length 2·28–4·4 mm (eight specimens).

In one male, having the same carapace length as the holotype, the cheliceral horn protrudes beyond the clypeus and may be clearly seen in dorsal view (Fig. 15C). Also, as in the case of *C. papuanus* the cymbium bears either two or three peg-like spines.

DISTRIBUTION. Papua New Guinea.

MATERIAL EXAMINED. **Papua New Guinea**: Louisiade Archipelago, Sudest Island, (*L. J. Brass*, Fifth Archbold Expedition to New Guinea) (AMNH, New York): Rambuso, on north coast, 0–100 m, holotype ♂, camp 11, xiii.1956; Mt. Riu, paratype ♂, 250–350 m, 1956. Kokoda, paratype ♂, viii.1933 (*L. E. Cheesman*) (BMNH. 1934.12.14.269); Morobi Province, Buro river, paratype ♂, ix.1979 (*J. H. Martin*) (BMNH. 1981.7.31.1); Milne Bay, paratype ♂, autumn 1944 (*R. B. Burrows*, A.P.O. 928) (AMNH, New York); Oro Bay; paratypes 2♂♂, (Lt. *B. Struck*, A.P.O. 503) (AMNH, New York), paratype ♂, vii–viii.1943 (*Sidney Sandler*) (AMNH, New York).

Genus ***ALLOCOCALODES*** gen. n.

DEFINITION. Based on two species known only from males.

Spiders of medium size (i.e. 4·0 to 8·0 mm in length). Male with elongate and porrect chelicerae bearing a median horn which is sometimes visible in dorsal view; not hirsute. *Carapace*: profile as in Figs 16A, B; 17A, B); high, longer than broad, with steep thoracic slope, widest at level of coxae II–III; fovea long, sulciform, centre situated just behind posterior margin of posterior lateral eyes. *Eyes*: large with black surrounds except anterior medians; posterior median and posterior laterals set on pronounced tubercles; set in three transverse rows comprised of anterior medians (AM) and anterior laterals (AL), posterior medians (PM) and posterior laterals (PL); anteriors contiguous with apices procurved in frontal view and recurved in dorsal view; anterior medians largest; anterior laterals greater than half diameter of anterior medians; posterior medians large, positioned nearer to anterior laterals than to posterior laterals and more or less on optical axis of anterior laterals; posterior laterals about as large as anterior laterals and set inside lateral margins of carapace when viewed from above; quadrangle formed by posterior medians and posterior laterals broader than long and widest posteriorly; entire quadrangle, measured from between bases of anterior medians to posterior margins of posterior laterals, occupying between 60–65% of carapace length. *Clypeus*: between 25 and 37% of diameter of anterior median eyes. *Chelicerae*: elongate and porrect, sometimes diverging, with a median horn arising basally; promargin with four teeth, retromargin with two. *Maxillae* (Fig. 16C): long and diverging with rounded apices. *Labium*: oblong about half maxillae length. *Sternum* (Fig. 16C): scutiform. *Coxae*: I and II largest. *Pedicel*: short. *Abdomen*: elongate ovoid; spinnerets moderately long, posteriors longest with moderately long apical articles, anteriors robust, slightly longer than more slender medians; spiracle a transverse slit just in front of anterior spinnerets; tracheal system not examined; position of colulus indicated by scanty tuft of fine hairs; anal tubercle a broad cone. *Legs*: long and slender; spines moderately strong and numerous; claws pectinate; tufts present; scopulae absent. *Male palps*: moderately simple and similar in appearance; femora slightly bowed; patellae moderately long; tibiae with small dorsal tubercle, bifid retrolateral apophysis, the ventral element broad and rounded, the dorsal slender with translucent tip; cymbium with distal finger-like extension and shallow dorsally ridged excavation on retrolateral basal margin; embolus (e) short, moderately stout and curved, arising subapically; functional conductor (c) a finger-like extension of the tegulum the tip of which lies either above or below that of the embolus; also arising from tegulum a lobe-like median apophysis (m); tegulum (t) ovoid with peripheral seminal ducts and what appears to be an inner folded duct. Expanded palps not examined.

Type species. *Allococalodes alticeps* sp. n.

Affinities. Closely related to *Cocalodes*, see remarks on p. 264.

Diagnosis. From *Cocalodes* by the bifid retrolateral tibial apophysis, lobe-like functional conductor and median apophysis (Figs 16E; 17C).

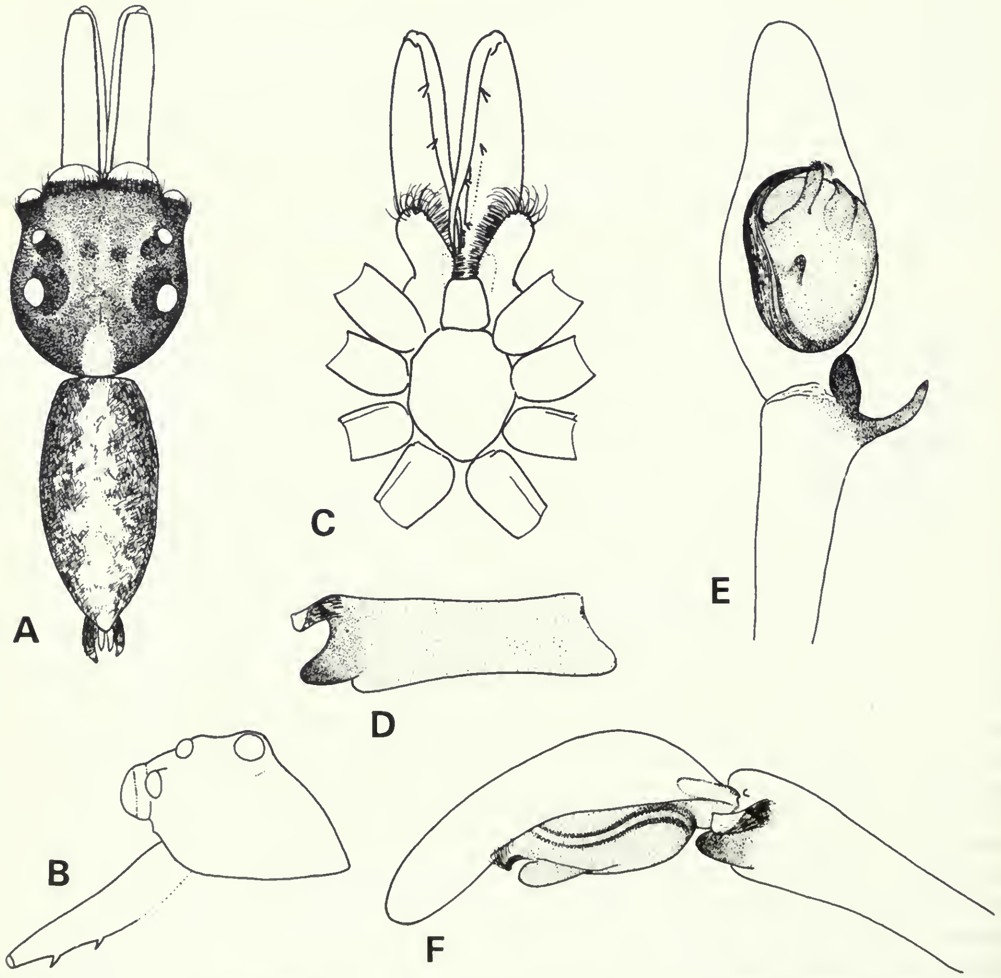

Fig. 16 *Allococalodes alticeps* sp. n. Holotype ♂: A, dorsal; B, carapace lateral; C, sternum, coxae and mouth parts; D, palpal tibia, retrolateral; E, palp, ventral; F, palp, retrolateral.

List of species in the genus *Allococalodes* gen. n.

Allococalodes alticeps sp. n.
A. cornutus sp. n.

Allococalodes alticeps sp. n.
(Fig. 16A–F)

DIAGNOSIS. From *A. cornutus* by the pointed tip of the median apophysis (Fig. 16E).

FEMALE. Unknown.

MALE HOLOTYPE. In fair condition. *Carapace* (Fig. 16A, B): dark chestnut brown with central yellow-brown thoracic band and vague yellow-brown markings in eye region; sides clothed in short recumbent amber hairs, iridescent under some angles of illumination, with whitish hairs on thoracic band and eye region. *Eyes*: with black surrounds except AM; fringed by whitish hairs. *Clypeus*: fringed in white hairs. *Chelicerae*: elongate and porrect; dark brownish orange with blackish mottling; thinly clothed in stiff light amber hairs; promargin with four teeth, retromargin with two; cheliceral horn protruding just beyond clypeal margin, but not visible in dorsal view. *Maxillae and labium*: brownish orange suffused black with inner margin of maxillae and labial tip dull yellow-brown. *Sternum*: brownish orange suffused black. *Coxae*: yellow-brown. *Abdomen*: mottled black with dorsal light yellow band somewhat broken and having blackish markings; clothed in minute dull whitish hairs; spinnerets tinged black, the posteriors with lighter terminal articles. *Legs*: generally yellow-brown with blackish annuli; spines strong and numerous. Spination of legs I: metatarsi v 2–0–1, p 1–1–1, r 1–1–1; tibiae v 2–2–2, p 1–1–1, d 1–1–0, r 1–1–1; patellae p 0–1–0, r 0–1–0; femora p 1–1–1, d 0–2–2, r 0–1–0. *Palp* (Fig. 16D, E): when viewed from below (i.e. Fig. 16E), the tip of the embolus lies above the tip of the functional conductor (c.f. *A. cornutus*).

Dimensions (mm): total length 4·84; carapace length 2·2, breadth 2·04, height 1·64; abdomen length 2·56; eyes, anterior row 1·96, middle row 1·68, posterior row 1·8; quadrangle length 1·44 (65% of carapace length). *Ratios*: AM : AL : PM : PL :: 16 : 10 : 6·5 : 10; AL–PM–PL :: 8–10; AM : CL :: 16 : 4 (25% of AM diameter).

DISTRIBUTION. Irian Jaya.

MATERIAL EXAMINED. **Irian Jaya**: Sukarnapura (Hollandia), rain forest, holotype ♂, 31.xii.1944 (*L. W. Saylor*) (AMNH, New York).

Allococalodes cornutus sp. n.
(Fig. 17A–E)

DIAGNOSIS. From *A. alticeps* by the obtuse tip of the median apophysis (Fig. 17C).

FEMALE. Unknown.

MALE HOLOTYPE. In poor condition. *Carapace* (Fig. 17A, B): dark orange-brown with pale eye region and median light yellowish brown thoracic band from foveal area to posterior margin; sides clothed in short recumbent amber hairs, shining under some angles of illumination, with dull whitish hairs on thoracic band and eye region. *Eyes*: with black surrounds except AM; fringed by dull whitish hairs. *Clypeus*: White haired. *Chelicerae*: elongate, porrect and diverging; dark orange-brown with blackish mottling; sparsely clothed in fine clear whitish hairs; promargin with four teeth, retromargin with two; cheliceral horn spiralled and protruding beyond clypeal margin. *Maxillae*: brown-black to dirty yellow-brown. *Labium*: dark brownish. *Sternum*: amber with irregular blackish mottling. *Coxae*: yellow-brown. *Abdomen*: damaged; elongate ovoid; yellow-brown with irregular blackish markings. *Legs*: generally light orange-brown grading

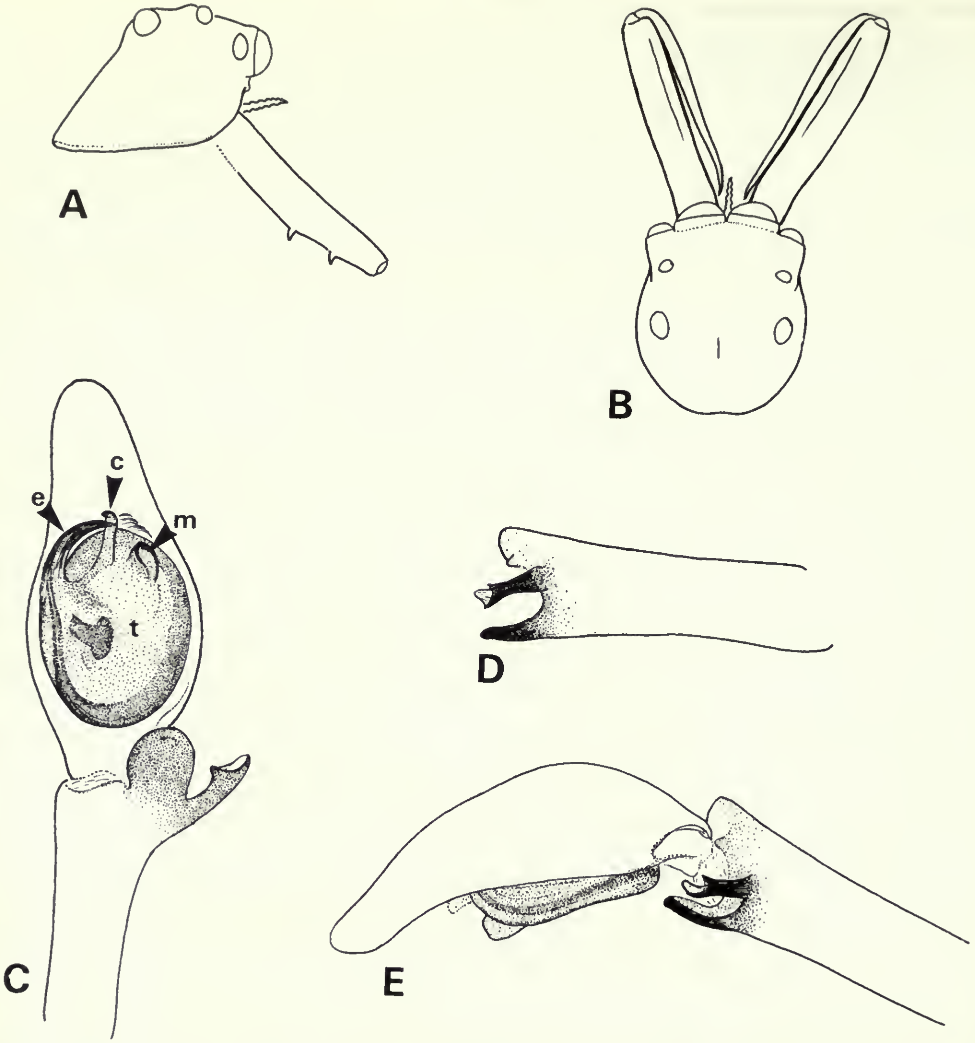

Fig. 17 *Allococalodes cornutus* sp. n. Holotype ♂: A, carapace lateral; B, carapace, dorsal; C, palp, ventral; D, palpal tibia, retrolateral; E, palp, retrolateral. Abbreviations: c, functional conductor; e, embolus; m, median apophysis; t, tegulum.

to yellow-brown distally with blackish annuli; spines moderately strong and numerous. Spination of legs I: metatarsi v 2–1–1, p 1–1–1, d 0–0–1, r 1–0–1; tibiae v 2–4–1, p 1–1–1, d 1–1–0, r 1–1–0; patellae p 1–0–0, r 1–0–0; femora p 1–1–0, d 0–2–2. *Palp* (Fig. 17C–E): when viewed from below the functional conductor lies above the embolic tip (Fig. 17C).

Dimensions (mm): total length c. 4·8; carapace length 2·32, breadth 2·02, height 1·66; abdomen length c. 2·6; eyes, anterior row 1·94, middle row 1·62, posterior row 1·76; quadrangle length 1·4 (60% of carapace length). *Ratios*: AM : AL : PM : PL :: 15: 9 : 6·5 : 9·5; AL–PM–PL :: 9–9; AM : CL :: 15 : 5·5 (37% of AM diameter).

DISTRIBUTION. Irian Jaya.

MATERIAL EXAMINED. **Irian Jaya,** holotype ♂, (*Dr. Moszkowski,* no 54) (MNHU, Berlin. 17800).

Taxonomic summary

1. *Allococalodes* gen. n., is proposed.
2. Eight new species are described:
    - *Allococalodes alticeps* sp. n.
    - *Allococalodes cornutus* sp. n.
    - *Cocalodes cygnatus* sp. n.
    - *Cocalodes expers* sp. n.
    - *Cocalodes innotabilis* sp. n.
    - *Cocalodes longicornis* sp. n.
    - *Cocalodes platnicki* sp. n.
    - *Cocalodes turgidus* sp. n.
3. Three species are newly synonymized:

    Cocalodes armatissimus Strand, 1913, and *Cocalodes plebejus* Szombathy, 1915, are junior synonyms of *Cocalodes papuanus* Simon, 1900.

    Cocalodes melanognathus Pocock, 1897, is a junior synonym of *Cocalodes leptopus* Pocock, 1897.

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I wish to thank the following colleagues for providing specimens for study. Dr Gianna Arbocco, Museo Civico di Storia Naturale, Genova, Italy (MCSN, Genova); Dr M. Grasshoff, Forschungsinstitut Senckenberg, Natur-Museum, Senckenberg, Frankfurt am Main, West Germany (FS, Frankfurt am Main); Dr M Hubert, Muséum National d'Histoire Naturelle, Paris, France (MNHN, Paris); Dr H. W. Levi, Museum of Comparative Zoology, Harvard, U.S.A. (MCZ, Harvard); Dr M. Moritz, Museum für Naturkunde der Humboldt-Universitat, Berlin, East Germany (MNHU, Berlin); Dr N. I. Platnick, American Museum of Natural History, New York, U.S.A. (AMNH, New York).

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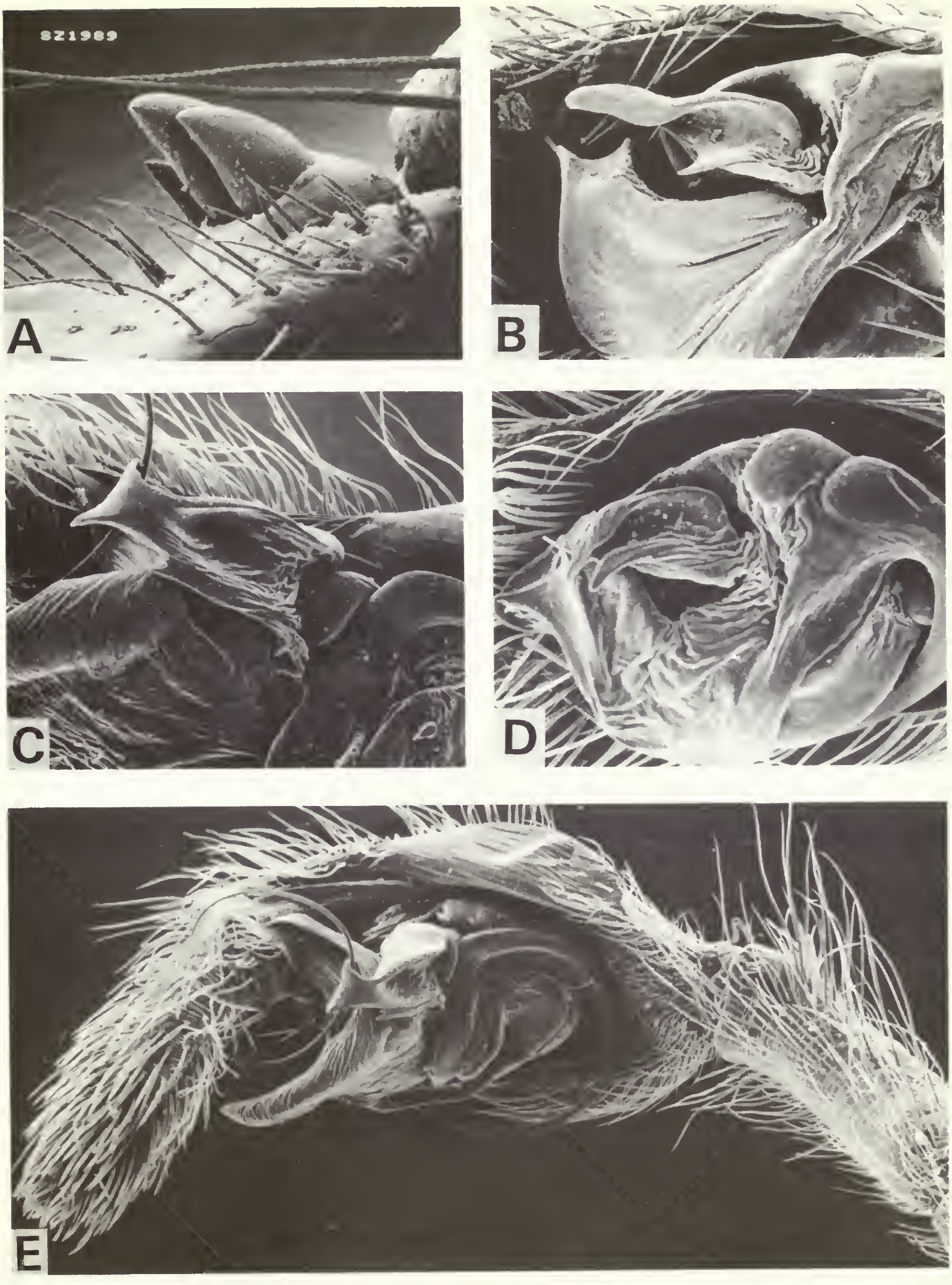

Fig. 18 (A, B) *Cocalodes innotabilis* sp. n. ♂ palp: A, peg-like cymbial spines, ×500; B, median apophysis and functional conductor, ×100. (C, E) *C. papuanus* Simon. ♂ palp: C, median apophysis, ×100; E, ventrolateral view, ×60. (D) *C. thoracicus* Szombathy. ♂ palp, median apophysis, ×150.

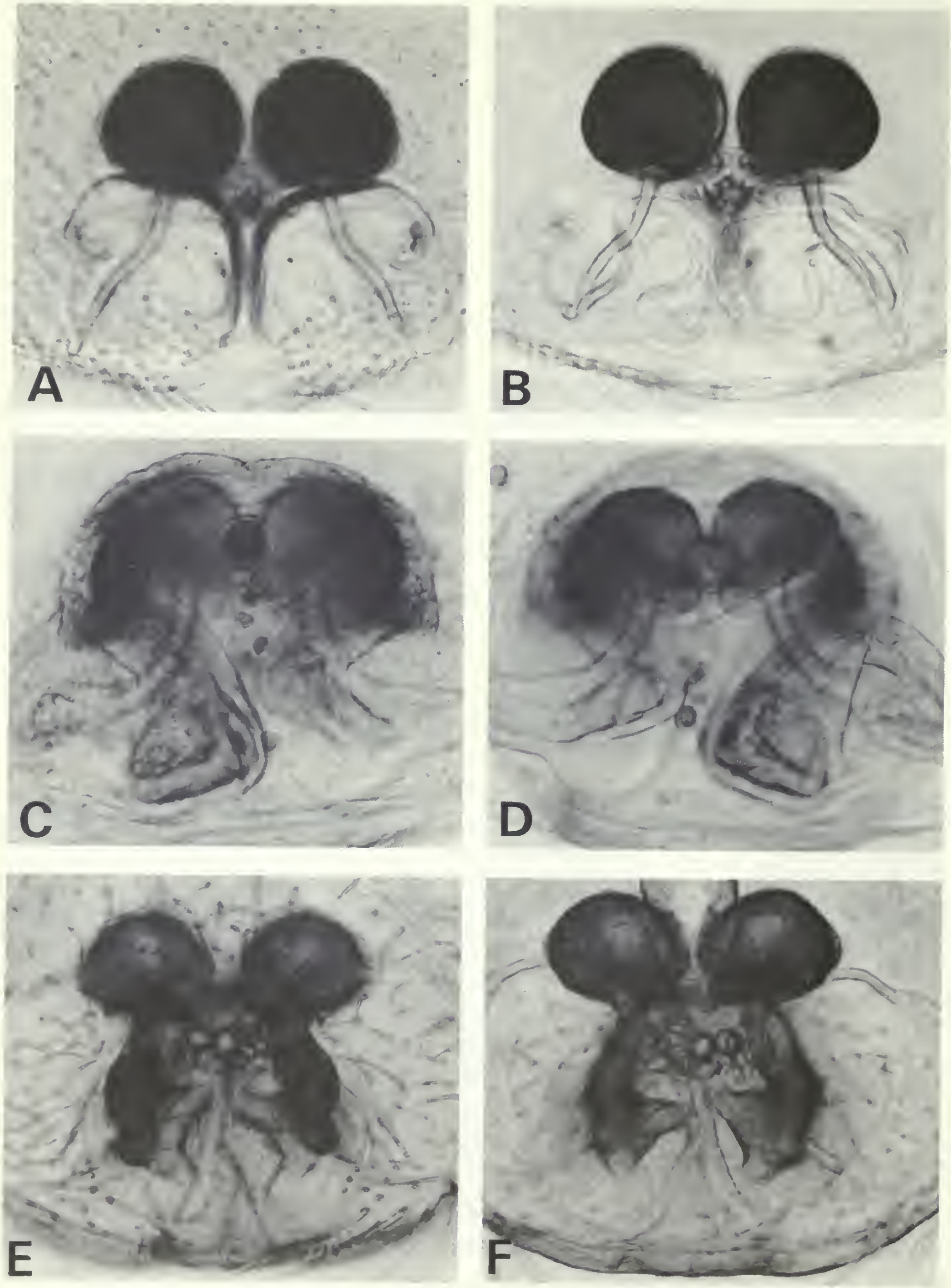

Fig. 19 (A, B) *Cocalodes papuanus* Simon. Vulva: A, ventral; B, dorsal, ×100. (C, D) *C. leptopus* Pocock. Vulva: C, ventral; D, dorsal, ×140. (E, F) *C. cygnatus* sp. n. Vulva: E, ventral; F, dorsal; ×140.

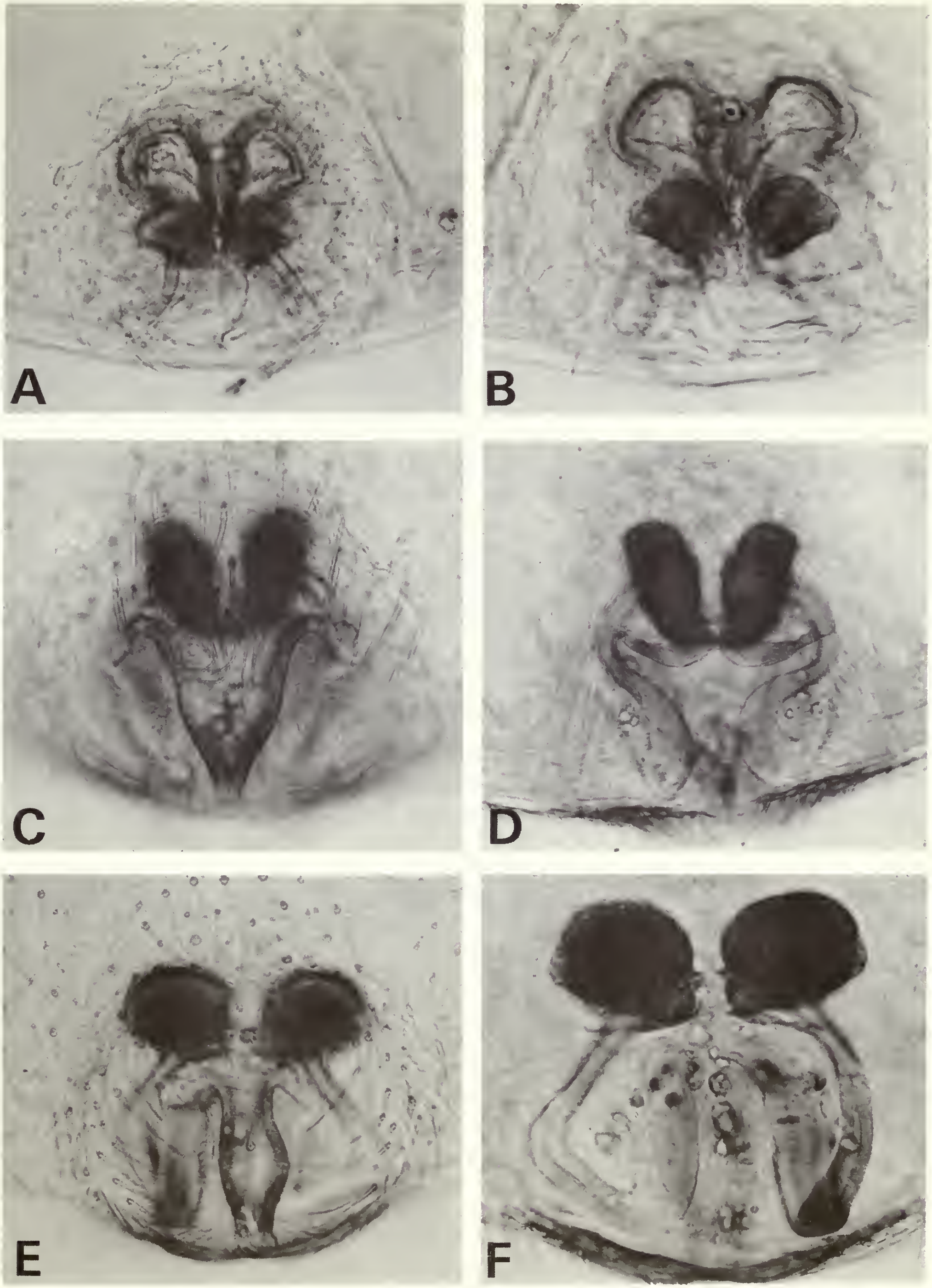

Fig. 20 (A, B) *Cocalodes macellus* (Thorell). Vulva: A, ventral; B, dorsal; ×100. (C, D) *C. thoracicus* Szombathy. Vulva: C, ventral; D, dorsal; ×100. (E, F) *C. turgidus* sp. n. Vulva: E, ventral, ×100; F, dorsal, ×135.

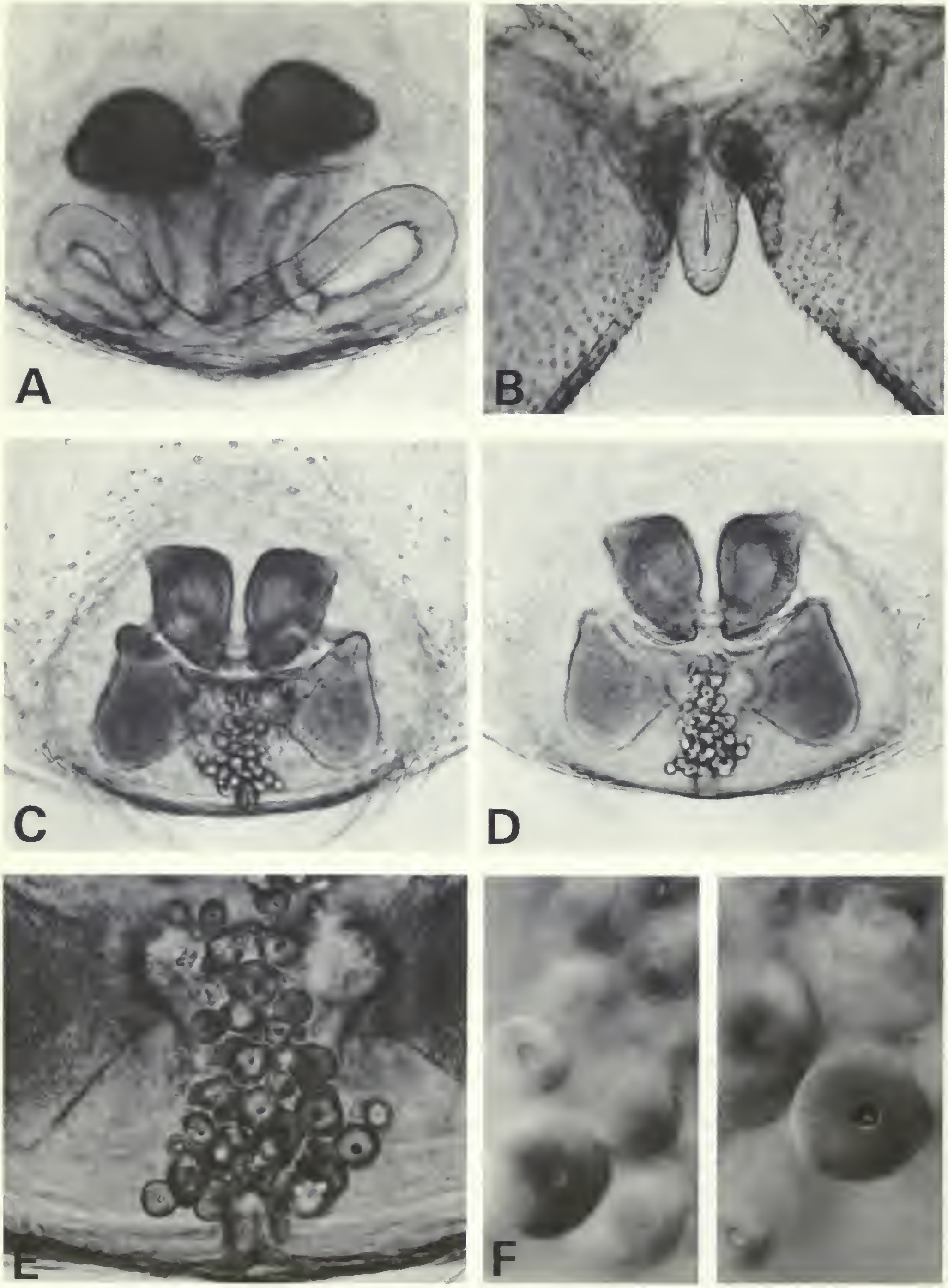

Fig. 21 A, *Cocalodes longicornis* sp. n., vulva dorsal view, ×140. B, *C. papuanus* Simon, cheliceral horn, ×85. (C, D) *C. platnicki* sp. n. Vulva: C, ventral; D, dorsal; ×100. (E, F) spherical bodies in vulva of *C. platnicki*; E, ×280; F, ×1200.

Anatomy and evolution of the jaws in the semiplotine carps with a review of the Genus *Cyprinion* Heckel, 1843 (Teleostei: Cyprinidae)

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Introduction

Scant attention has been paid to the jaw anatomy of cyprinid fishes. Takahasi (1925) described the jaw musculature of various cyprinoids, but only Matthes (1963) and Alexander (1966) have described the osteo-myological anatomy of the cyprinid jaw. These authors, and Ballantijn (1969), have also attempted a functional interpretation of particular jaw types. Howes (1978, 1979, 1980, 1981) described and commented on jaw types of (mostly) non-barbelled carps ('Leuciscinae'). But, in these studies the potential value of the jaws as indicators of phyletic relationship was not recognised. The more diverse jaw morphology of barbelled carps ('Cyprininae') has, however, focussed attention on this aspect of jaw anatomy.

From among the 'Cyprininae' the genus *Semiplotus* is chosen as a model for detailed description because member species possess what is an obviously highly derived osteo-myological jaw structure, manifest externally in the size and shape of the mouth (see below). *Semiplotus* species are large (according to Day (1889) *S. semiplotus* attains at least 2 feet in length), distinctive carps whose geographical range extends through northern India and Burma. The distinctiveness of these fishes lies in the size and shape of the head and extreme body depth (Figs 1A–C). Likewise, the mouth is of great width (probably the widest mouth in relation to head length of any cyprinid fish), the lower jaw is edged with a cornified epithelium and is overhung by the upper jaw (Figs 1B & C).

Many cyprinid taxa possess broad, ventral mouths with cornified cutting edges, the so-called 'sector mouth' (see p. 313 for definition). Only in *Onychostoma, Varicorhinus, Capoeta* and *Cyprinion* does the morphology of the mouth approach that of *Semiplotus*, both in width and complex development of the lower lip.

Members of these genera are compared here in order to test the hypothesis that a sector mouth is synapomorphic for the group and also to elucidate the possible evolutionary pattern of semiplotine jaw modification.

Nomenclatural note

In the anatomical descriptions, *Scaphiodonichthys burmanicus* is referred to as *Semiplotus burmanicus*. The existence in both 'genera' of synapomorphic osteological and myological characters indicates their generic unity (see p. 312 for a list of characters, and p. 331 for complete synonymy). No specimens of *Semiplotus modestus* have been examined and reference to '*Semiplotus*' in the anatomical text refers only to the species *semiplotus* and *burmanicus*.

List of specimens used in anatomical description

Capoeta capoeta	BMNH 1968.12.13 : 405–416
Capoeta capoeta	BMNH 1879.11.14 : 19 (skeleton)

Bull. Br. Mus. nat. Hist. (Zool.) **42** (4) : 299–335 Issued 24 June 1982

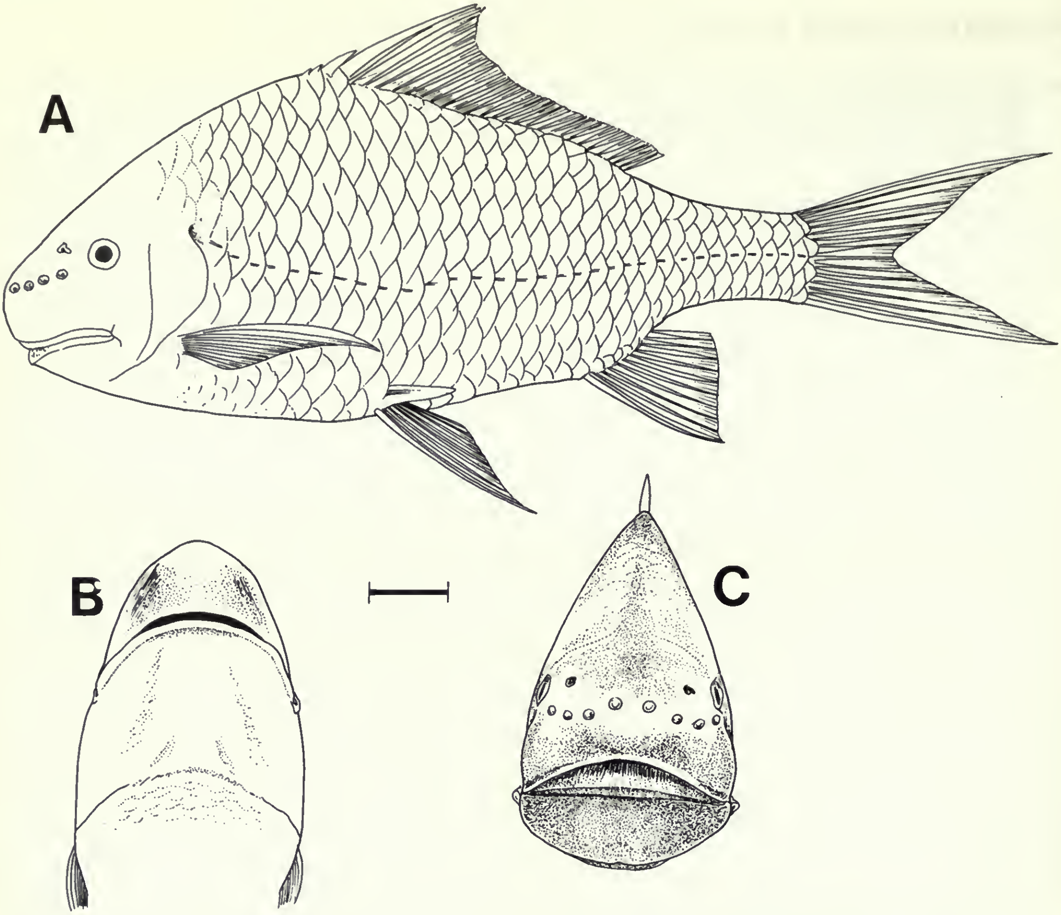

Fig. 1 *Semiplotus semiplotus*. A, in lateral view. B & C, ventral and anterior aspects of the head. Scale = 10 mm. Drawn from specimen 1889.2.1 : 365 – 6.

Capoeta fusca	BMNH 1899.7.15 : 26
Cyprinion acinaces	BMNH 1977.8.25 : 1–5
Cyprinion kais	BMNH 1974.2.22 : 1115–8
Cyprinion macrostoma	BMNH 1974.2.22 : 118–95
Cyprinion microphthalmum	BMNH 1883.8.2 : 4–9
Cyprinion microphthalmum	BMNH 1977.12.13 : 532–545; 546–556
Cyprinion milesi	BMNH 1889.2.1 : 263–4
Cyprinion watsoni	BMNH 1889.2.1 : 387–396
Cyprinion watsoni	BMNH 1913.4.15 : 90–99
Onychostoma laticeps	BMNH 1969.4.15 : 105–110
Onychostoma varus	BMNH 1935.4.18 : 22
Semiplotus burmanicus	BMNH 1893.2.16 : 32 (skeleton)
Semiplotus burmanicus	BMNH 1889.10.4 : 2
Semiplotus burmanicus	BMNH 1920.9.8 : 1–3
Semiplotus burmanicus	Uncat. Smithsonian Colln.
Semiplotus semiplotus	BMNH 1889.2.1 : 365–6
Semiplotus semiplotus	BMNH 1889.2.1 : 367 (skeleton)
Semiplotus semiplotus	BMNH 1972.7.26 : 10
Squaliobarbus curriculus	BMNH 1888.5.15 : 29 (skeleton)

Varicorhinus beso	BMNH 1968.7.24 : 2
Varicorhinus beso	BMNH 1968.7.24 : 17–19 (alizarins)
Varicorhinus beso	BMNH 1902.12.13 : 377 (skeleton)
Varicorhinus tanganicae	BMNH 1906.9.6 : 11 (skeleton)

Abbreviations used in text figures

A_1a, A_1b, A_2, A_3, A_w	Divisions of the *adductor mandibulae* muscle
Aa	Anguloarticular
Aamp	Aponeurosis of *adductor mandibulae* and *protractor hyoideus* muscles
Aap	Premaxillary anterior ascending process
Afl, 2, 3	Articulatory facets of anguloarticular
Ahy	Anterohyal
Ama	Aponeurosis of *adductor mandibulae* A1 muscle
Ao	*Adductor operculi* muscle
Apl, 2	Articulatory processes of anguloarticular
Br	Branchiostegal ray (numbered)
Cm	Coronomeckelian bone
Cp	Coronoid process of dentary
Ctls	Labial shelf connective tissue
Cts-fef	Connective tissue strand linking maxilla to frontal-ethmoid foramen
De	Dentary
Dhy	Dorsohyal
Do	*Dilatator operculi* muscle
Ect	Ectopterygoid
Elt	Epithelial layer of lower lip
Ent	Entopterygoid
Epo	Epioccipital
Etb	Epithelial tendinous layer
Exo	Exoccipital
Fr	Frontal
Fsef	Frontal-supraethmoid foramen
Hy	Hyomandibula
Ic	Intercalar
Ihy	Interhyal
Im	*Intermandibularis* muscle
Iop	Interoperculum
Iopf	Interopercular facet
Ke	Kinethmoid
Ks	Keratinized lip surface
Lac	Ligament linking retroarticular with anterohyal
Lai	Ligament linking retroarticular with interoperculum
Lap	*Levator arcus palatini* muscle
Lapo	Ligament linking retroarticular with preoperculum
Laq	Ligament linking anguloarticular with quadrate
Le	Lateral ethmoid
Lkee	Ligament linking kinethmoid to ethmoid
Lkmx	Ligament linking kinethmoid to maxilla

Lkp	Ligament linking kinethmoid to palatine
Lkpm	Ligament connecting kinethmoid to premaxilla
Ll	Lower lip
Llm	Lateral lamellae
Lo	*Levator operculi* muscle
Lpe	Ligament linking palatine to ethmoid
Lpm	Ligament linking palatine to maxilla
Lqu	Ligament linking quadrate to interoperculum
Ls	Labial shelf
Mdp	Maxillary distal process
Me	Mesethmoid
Met	Metapterygoid
Mfp	Medial fatty partition
Mkl	Medial keratinized layer of lower lip
Mlp	Maxillary mid-lateral ascending process
Mlt	Medial tissue layer of lower lip
Mmp	Medial maxillary process
Mn	Medial notch
Mv	Maxillary valve
Mx	Maxillary
Mxf	Maxillary foramen
Mxn	Maxillary notch
Nc	Neural complex
Ns	Neural spines
Op	Operculum
Pa	Parietal
Pal	Palatine
Pe	Preethmoid
Ph	*Protractor hyoideus* muscle
Pha	Medial aponeurosis of *protractor hyoideus*
Phat	Anterior tendinous segment of *protractor hyoideus*
Phav	Antero-ventral segment of *protractor hyoideus*
Phbt	Basal tendinous layer of *protractor hyoideus*
Phd	Dorsal segment of *protractor hyoideus*
Phl	Lateral segment of *protractor hyoideus*
Phlt	Lateral tendon of *protractor hyoideus*
Phpv	Postero-ventral segment of *protractor hyoideus*
Phy	Posterohyal
Pop	Preoperculum
Pro	Prootic
Ps	Parasphenoid
Pte	Pterotic
Pty	Pterygiophore (dorsal)
Q	Quadrate
Qaf	Quadrate anterior facet
Qlf	Quadrate lateral facet
Qmb	Quadrate medial buttress
Ra	Retroarticular
Se	Supraethmoid
Sh	*Sternohyoideus* muscle
Sj	Synarthritic mandibular joint
Sn	Supraneurals (numbered)
Soc	Supraoccipital
Socr	Supraoccipital crest

Stf	Subtemporal fossa
Sy	Symplectic
Syf	Symplectic facet
TA2-1b	Tendon connecting A_2 with A_1b
TA3	Insertion tendon of *adductor mandibulae* A_3
Ur	Urohyal
V	Vomer
Velt	Ventral epithelial lip tissue
Vhy	Ventrohyal
Vmlt	Ventral medial tissue layer of lower lip

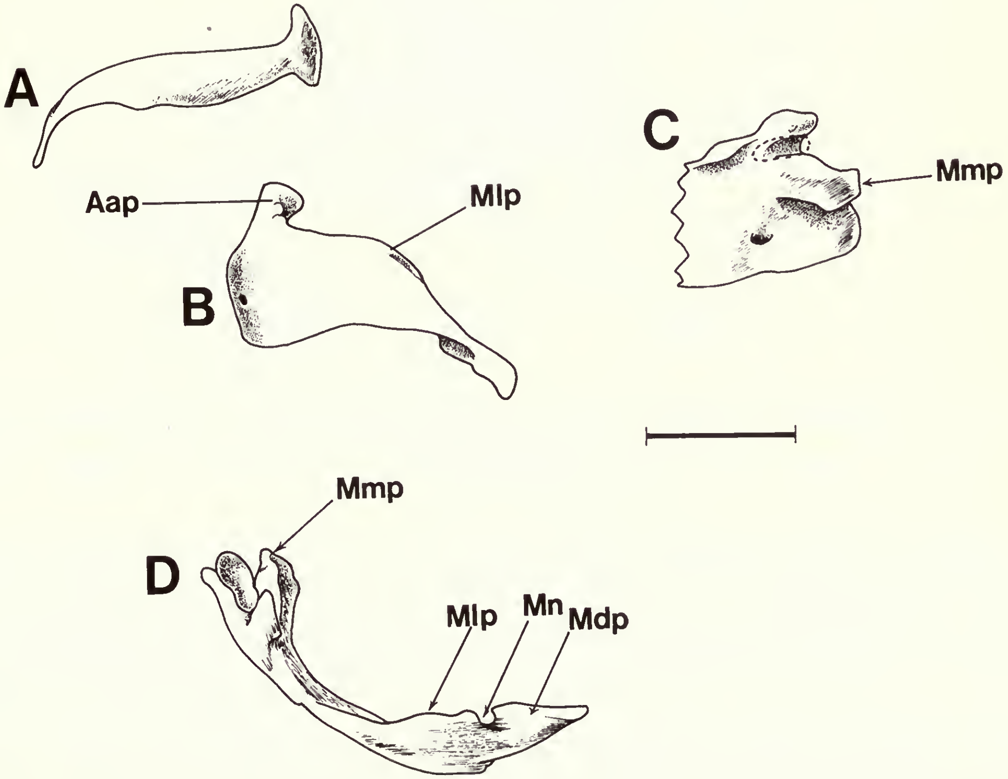

Fig. 2 *Semiplotus semiplotus*, upper jaw bones. A, premaxilla, lateral view. B, maxilla, lateral view. C, maxilla, medial view of symphysial portion; dashed line indicates meniscus. D, maxilla, dorsal view. Scale = 10 mm.

Jaw anatomy of *Semiplotus semiplotus* (McClelland, 1839)

Upper jaw bones

The *premaxilla* (Fig. 2A) is exceedingly thin and shallow, with only a slight anterior ascending process. The posterior portion of the bone is directed ventrally at a right angle to its anterior part, with its tip compressed and shallowly bifurcated.

The *maxilla* (Fig. 2B) is deep, its dorsal border convex. The anterior ascending process (Aap) is shallow and thick, its dorsal border notched (the palatine ligament lies across this notch). The upper symphysial border of the ascending process is turned so that its face forms a 45° angle to the midline. The lower portion is strongly concave and extends anteromedially to form the symphysial part to the maxilla, syndesmotically contacting its partner. The medial (rostral) maxillary process (Mmp, Fig. 2C) is almost square and it too makes syndesmotic contact with its partner. A mid-lateral ascending process is represented by a slight convexity of the maxillary dorsal border (Mlp). This part of the maxilla is separated from the posterior part by a medial notch (Mn). The posterior rim of the notch acts also as the leading border of a broad medial triangular ledge.

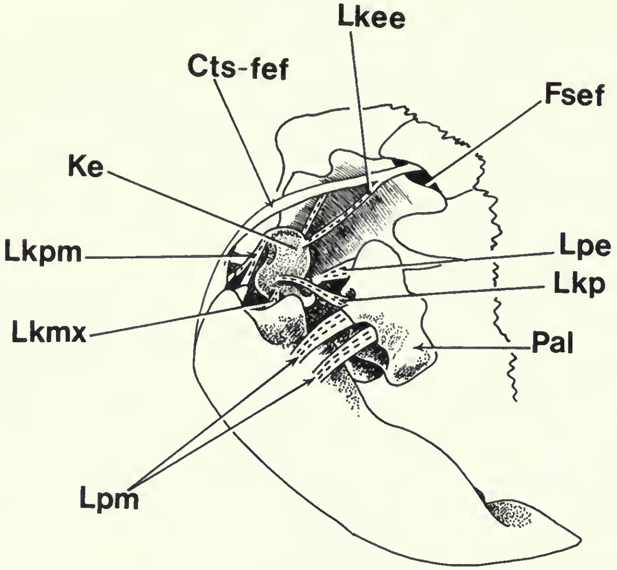

Fig. 3 *Semiplotus semiplotus,* upper jaw articulation in oblique dorso-lateral aspect. Scale = 5 mm.

Articulation of the upper jaw (Fig. 3)

The upper jaw bones articulate with the cranium *via* the kinethmoid, the palatine and the premaxillary meniscus.

The *kinethmoid* (Ke) is attached *via* a thick ligament from its head to the ascending process of the premaxilla (Lkpm). A broad, bifurcated ligament (Lkee) extends from the posterior face of the kinethmoid to attach to the lateral edges of the supraethmoid and, dorsally, to the connective tissue overlying the ethmoid region. A strand of this connective tissue (Cts-fef) inserts onto the rim of the foramen between the frontals and the supraethmoid. A mid-lateral ligament (Lkp) attaches the kinethmoid to the palatine, and a ventro-lateral ligament (Lkmx) links it to the maxilla.

A paired ligament (Lpm) attaches the lateral face of the maxilla with the lateral shelf of the *palatine* (Pal). The palatine, in turn, is connected with the mesethmoid by a thick medially directed ligament (Lpe).

Interposed between the medial face of the maxilla, the preethmoid and part of the vomer is a cartilaginous meniscus (*sensu* Alexander, 1966). This is thick and ellipsoidal and lies between a ventral prominence of the premaxillary ascending process and the medial (rostral) process (Fig. 3).

Muscles attaching to the upper jaw (Fig. 4)

The *adductor mandibulae* A_1 muscle occupies only the lower half of the cheek, the area below the orbit and between it being filled with fatty connective tissue. The muscle is divisible into ventral and dorsal sections. The lower section, A_1b, originates from the lower border of the preoperculum, is thin and triangular, but with its ventral border thickly tendinous. Fibre alignment varies from 45° (ventrally) to almost horizontal (dorsally). At the posterior tip of the maxilla, the muscle section is constricted into a bifurcated tendinous

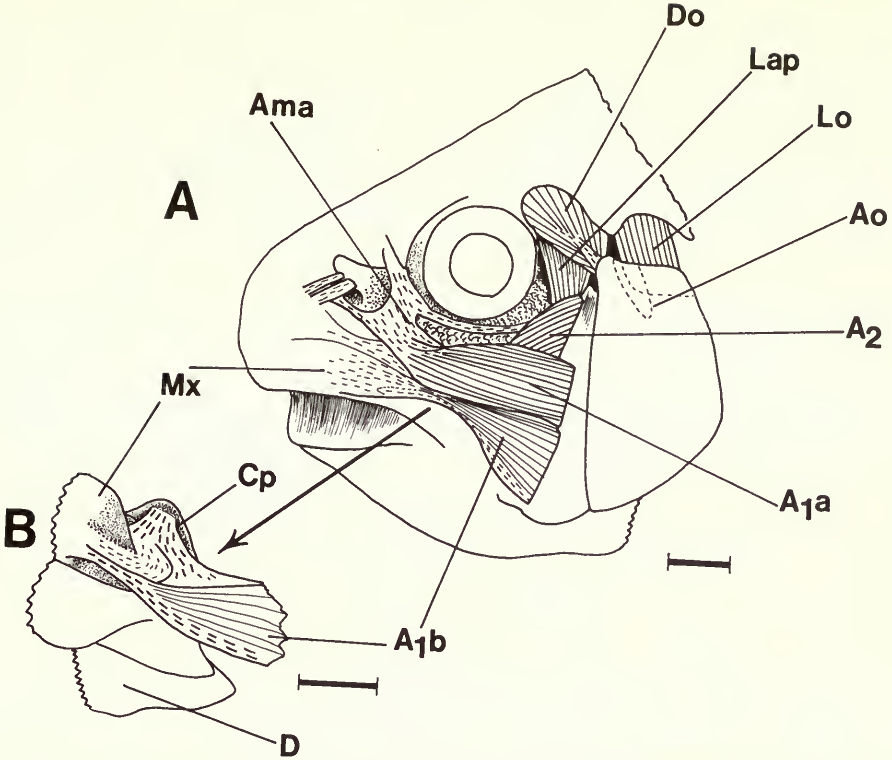

Fig. 4 *Semiplotus semiplotus.* A, lateral view of superficial jaw and cranial musculature. B, detail of jaw muscle insertions. Scale = 5 mm.

area, the outer tendon inserting on a small lateral maxillary process, the inner on the medial maxillary notch (see above, p. 304). The lateral border of the inner tendon (Fmd, Fig. 4B) extends mesially to attach to the lateral face of the dentary coronoid process. The medial fascia of adductor A_1b is connected with the lateral body of *adductor mandibulae* muscle A_2 by a thick tendon (see below).

The dorsal section of the *adductor mandibulae*, A_1a, originates from the central area of the preoperculum. This portion of the muscle is even thinner than A_1b, being only a few fibres in thickness at its origin. The segment is oblong, with an almost parallel arrangement of fibres. The muscle terminates *via* a narrow tendon which forms the lateral segment of a broad, thick aponeurosis (see below). The tendon of insertion reaches the first of the palatine-maxillary ligaments.

The aponeurosis into which muscle A_1a inserts is complex (Ama, Fig. 4). Laterally it is joined to the medial face of the 1st infraorbital, and medially to the lateral ethmoid and to the palatines. Ventro-medially the sheet has a posterior extension in the form of a tendinous band which joins onto the anterior edge of the entopterygoid and then expands to become continuous with the medial fascia of muscle A_3 (Fig. 8A).

Upper lip and buccal cavity (Fig. 9)
Epithelial tissue covering the upper jaw is thin and lacks a cornified edge. The inside of the mouth is bordered by a single row of leaf-like lamellae; above this row is a thin, narrow maxillary valve (Mv). The tissue covering the antero-lateral buccal roof is formed into a near longitudinal series of broad leaf-like lamellae (Llm). The surfaces of these lamellae are highly papillose. The vomerine tissue is transversly rugose; there is no vomero-palatine organ (*sensu* Matthes, 1963).

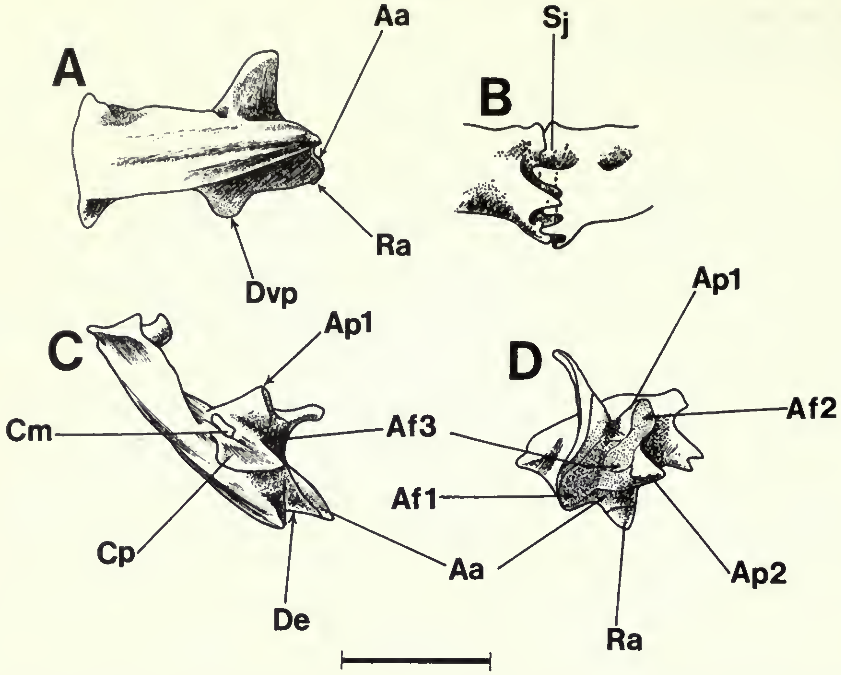

Fig. 5 *Semiplotus semiplotus,* lower jaw bones. A, lateral; C, dorsal; and D, posterior views. B, medial aspect of dentary joint. Dotted lines indicate the course of a ligamentous connection. Scale = 10 mm.

Lower jaw bones (Fig. 5)
Each *dentary* (Figs 5A & B) articulates with its partner *via* a complex symphysial joint (Sj). This is basically a peg and socket joint, the central peg being on the dentary of the right side and inserting into a deep notch in the left dentary. Above the joint there is a strong ascending process on each bone, joined syndesmotically to that of its partner. Ventrally, the articulation is more complex (Fig. 5B). Each dentary is extended as a ventral process which is joined to its counterpart *via* a bifurcated, curved articulation. Strong, vertical ligaments connect each facet of this joint.

The wall of the dentary is thick, its dorsal part tapering to a thin edge and curving mesially so as to form a sloped labial surface. On the medial underside of this lip is a deep cavity into which the *intermandibularis* muscle inserts. The lateral face of the dentary bears a deep ridge which tapers posteriorly to a V-shaped process. The coronoid process is high and almost square, its anterior edge curved outward so that when viewed dorsally (Fig. 5C) the plane of the dorsal margin of the coronoid is coincident with that of the body axis. The posterior border of the dentary is blunt with a rounded ventral process corresponding in position to the coronoid process (Dvp, Fig. 5A).

The *anguloarticular* (Aa, Figs 5C & D) is a large, triangular bone, its posterior dorsal edge extending someway up the medial face of the dentary coronoid process, following that processes' outward curvature. The articulatory surface is complex. Postero-laterally there is a triangular facet (Af1, Fig. 5D), its posterior border extending only slightly beyond that of the dentary. The medially directed portion of the anguloarticular is bifurcated. The dorsal process (Ap1) is thickly rounded and directed somewhat dorsally, its posterior face forming a facet (Af2). The ventral process (Ap2) is triangular and is directed slightly ventrally. The medial dorsal process (Ap1) is separated from the outer wall of the bone by a deep, concave channel. The posterior aspect of the anguloarticular is V-shaped and there is a large, figure of 8-shaped facet situated between the dorsal and ventral medial processes (Af3). In lateral view, only a narrow portion of the anguloarticular is visible beyond the posterior dentary margin.

The *retroarticular* (Ra, Fig. 5D) is a thick wedge lying below the ventral anguloarticular process (Ap2). Laterally, the retroarticular is almost entirely covered by the ventral process of the dentary and only a narrow portion is visible (Fig. 5A).

The *coronomeckelian* (Cm, Fig. 5C) is an almost oblong bone with a rounded posterior border. Its anterior portion projects medially to form a deep, sloped shelf. There is a slight depression on the shelf into which insert the tendons of the *adductor mandibulae* musculature.

Articulation of the lower jaw (Fig. 6)
The complex articulatory surface of the anguloarticular is matched by an equally complex *quadrate* surface.

The quadrate facet occupies the lateral anterior and medial portions of the bone (Figs 6B & C). The lateral facet (Lqf) is aligned at 45° to the horizontal and apposes the medial face of the lateral anguloarticular process (Afl). The anterior facet is also aligned at 45° and apposes

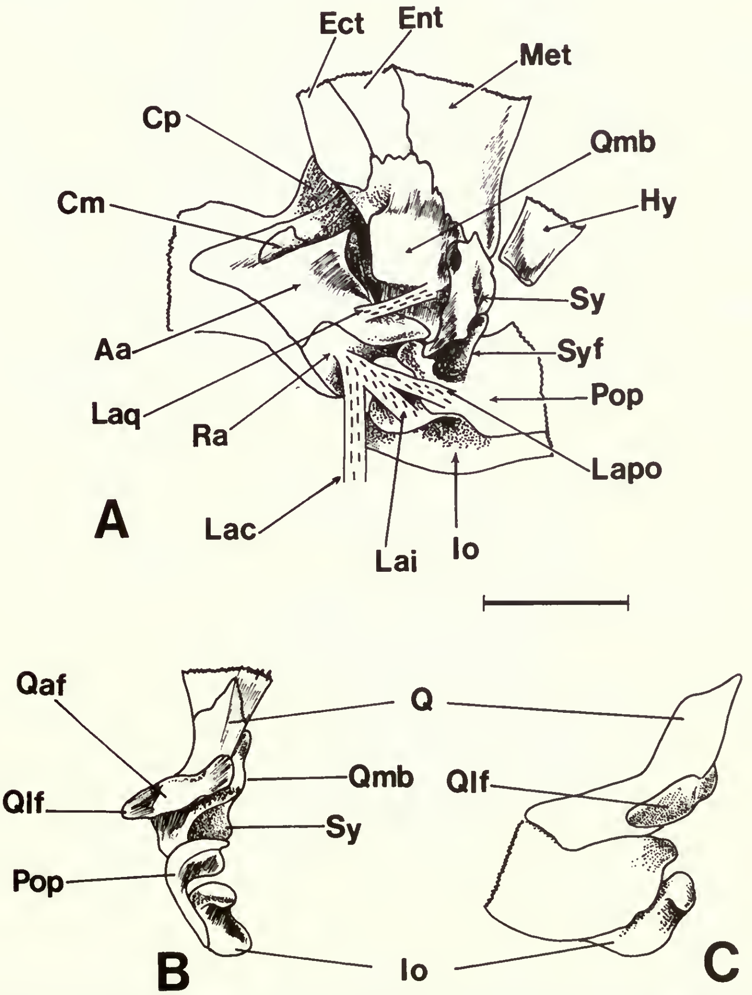

Fig. 6 *Semiplotus semiplotus*, lower jaw articulation. A, medial view of posterior jaw elements and their connections with suspensorial and opercular bones. B, anterior and C, lateral aspects of quadrate and inferior opercular elements. Scale = 5 mm.

the central anguloarticular facet (Af3). The medial part of the quadrate is formed into a buttress with an elliptical anterior face which apposes the dorso-medial anguloarticular facet (Af2). The ventro-medial process of the anguloarticular (Ap2) lies below the medial quadrate buttress and is attached to it by a thick ligament (Laq).

Ventrally a complexly divided ligament attaches the jaw to certain opercular and hyal elements. Immediately from its point of attachment to the posterior face of the retroarticular the ligament trifurcates and attaches, (1) to the anterior face of the interoperculum (Laio) which is medially curved and formed into a facet; (2) to the medial face of the preoperculum (Lapo) which is formed into a condyle; and (3) to the posterohyal *via* a fascial attachment to the ceratohyal (Lac).

The lateral articulations between the anguloarticular, preoperculum and interopercular bones is covered by a broad ligament which stems from the ventro-lateral face of the quadrate (Lqi, Fig. 8A).

Muscles attaching to the lower jaw (Fig. 7)

The muscles having their attachment to the lower jaw are the *adductor mandibulae* A_2 and A_3 (Fig. 7B). The upper portion of muscle A_2 originates from the hyomandibula and the

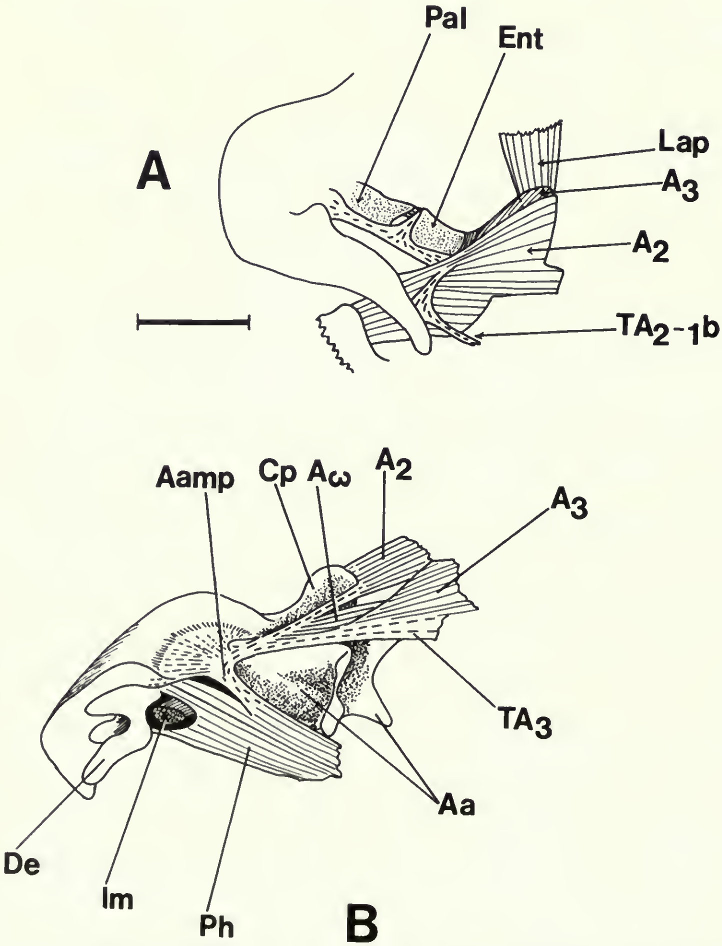

Fig. 7 *Semiplotus semiplotus*, lower jaw musculature. A, lateral view of the deeper muscle elements. B, medial view of jaw muscle insertions and their connection with hyoid musculature. Scale = 5 mm.

lower lateral portion of the preoperculum. All its fibres insert into a medial aponeurosis. From the lateral part of this aponeurosis a narrow tendon runs antero-ventrally into the medial fascia of the adductor muscle (A_1b (Fig. 7A). A bundle of fibres continues forward from the aponeurosis and almost immediately inserts into a thick tendon which terminates on the coronomeckelian bone (sesamoid articular). Insertion of A_2 is *via* a broad tendon onto the dorso-posterior rim of the dentary coronoid process. A thin, inner branch of the tendon continues ventrally down the medial face of the coronoid process to insert on the coronomeckelian bone. Attaching to this tendon is a triangular sheet of muscle fibres crossing from A_3; this most probably represents section A_w of the *adductor mandibulae* series (see Fig. 7B & p. 313).

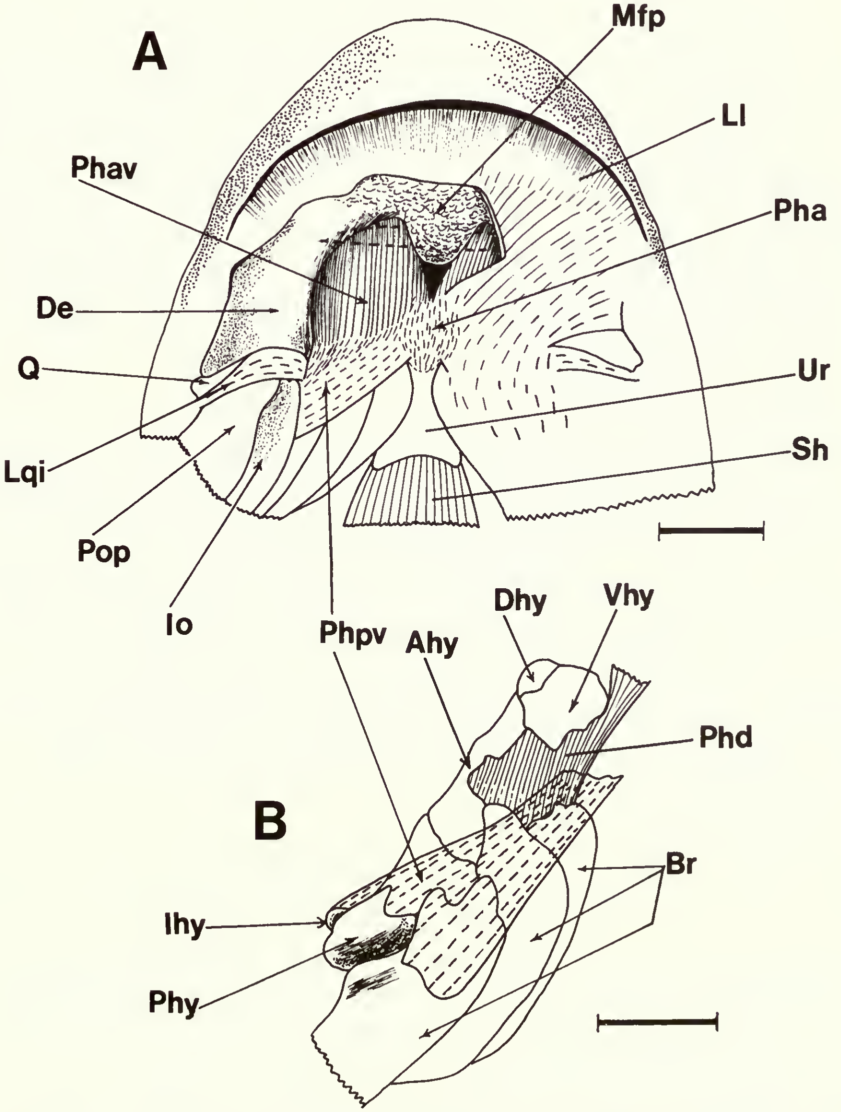

Fig. 8. *Semiplotus semiplotus,* hyoid musculature. A, ventral aspect of head with right side dissected to display major hyoid muscle elements. Dotted lines indicate path of the *intermandibularis* muscle. B, detailed view of *protractor hyoideus* insertions on hyoid elements of the right side. Scale = 5 mm.

Adductor mandibulae muscle A_3 originates partly from the hyomandibula (where it is separated from A_2 by the *levator arcus palatini* muscle) and partly from the deeply concave lateral face of the metapterygoid. Its fibres run almost at right angles to the midline to join the aponeurosis of muscle A_2. Antero-ventrally, A_3 inserts *via* a strong tendon which runs through the deep cleft between the medial and lateral portions of the anguloarticular, to join an aponeurosis on the coronomeckelian bone (Fig. 7B). Extending anteriorly from this aponeurosis is a set of thin, tendinous fibres which spread along the inner aspect of the dentary upper margin. These tendinous bands are connected by fibrous tissue to the overlying loose, fatty connective tissue of the lower lip (see below). From the lateral part of the aponeurosis a tendon extends ventro-posteriorly, across the medial face of the anguloarticular, to join the lateral portion of the *protractor hyoideus* muscle (Tcph, Fig. 7B).

The *protractor hyoideus* muscle is a short and thick element divisible into dorsal and ventral sections (Fig. 8A). The ventral portion is X-shaped, the two anterior arms separated by a thick nodule of fatty tissue and each attaching to the medial face of the dentary. Their posterior junction is a thick pad (Pha) from which radiate wide, tendinous bands to form the ventral face of the muscle. These bands insert into the posterior margin of the tissue forming the lower lip (see below). The posterior arms of the muscle are almost entirely tendinous and attach to the branchiostegal rays, and the inner faces of the posterohyal and the interhyal. Each dorsal section of the *protractor hyoideus* is broad and extends from the ceratohyal and the 1st branchiostegal ray to join the ventrohyal. The more medial fibres run into the body of the muscle and insert into the tendinous area just anterior to the ventrohyal (Fig. 8B).

The *intermandibularis* is a thin, cylindrical muscle crossing between the dentaries where it is contained in a small cavity. The muscle separates, transversly, the anterior portions of the *protractor hyoideus* (Figs 8B & 9B).

The lower lip (Fig. 9)

The lower lip of *Semiplotus semiplotus* is a complex structure composed of several tissue types which extend well beyond the outer face of the dentary. Its core is a deep shelf of dense collagenous tissue that surrounds the dentary (Ls). This labial shelf is enveloped in loose, stratified epithelium. The tissue that covers the dorsal surface of the labial shelf is comprised of a thick, fatty epidermal layer (Elt), and an underlying, more fibrous tissue (Mlt). The ventral surface of this tissue adheres to tendinous bands originating from the aponeurosis that incorporates the insertions of the *adductor mandibulae* and *protractor hyoideus* muscles (see above). Thus, toward the lateral part of each dentary the labial epidermis becomes united with jaw and hyoid tendinous elements and only at the symphysis is it firmly attached to each dentary. Anteriorly, where it passes around the leading edge of the labial shelf, the epidermis is thin and cornified, forming a chisel-edge to the jaw (Ks). Ventrally, the epidermis is attached to the labial shelf by thin strands of connective tissue. As it passes beneath the dentary the tissue becomes tendinous and contiguous with the ventral face of the *protractor hyoideus* (see above).

Apomorphic jaw characters in *Semiplotus*

Before considering whether, or to what degree, the jaws of *Semiplotus semiplotus* may be a derived feature, it is necessary to present a model of the plesiomorph cyprinid jaw and its associated articular elements for comparison. The following model is modified from Howes (1980, 1981) and is reckoned to be the plesiomorph type on grounds of its wide-spread occurrence amongst various cyprinid taxa.

The plesiomorph *maxilla* has a well-developed mid-lateral ascending process with convex anterior and concave posterior borders; the *premaxilla* L-shaped with a moderately developed anterior ascending process; *dentary* with a vertical, high, long coronoid process situated posteriorly; the *anguloarticular* with its dorsal border confluent with that of the dentary coronoid process but not extending to cover the medial face of that process, its

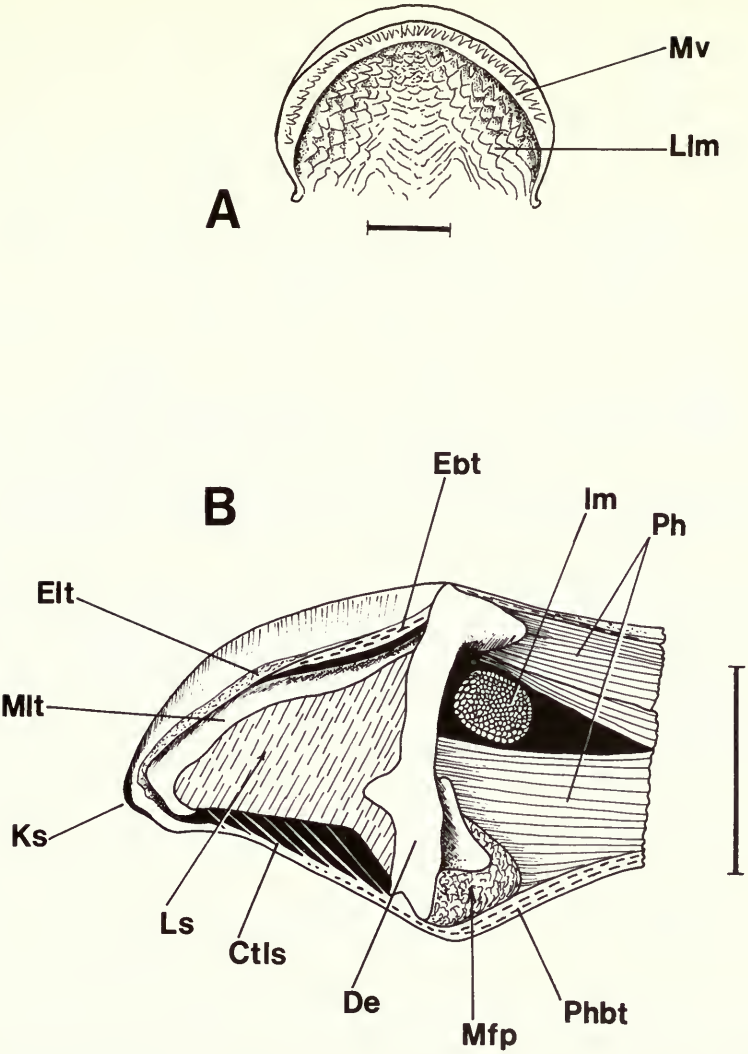

Fig. 9 *Semiplotus semiplotus*. A, ventral view of upper lip and buccal cavity. B, sagittal section through the lower lip and associated hyoid musculature. Scale = 5 mm.

posterior border reaching to well beyond the posterior margin of the dentary, its articulatory facet transversly concave. All those features are found in the jaws of *Squaliobarbus*, Fig. 10.

The plesiomorph cyprinid *quadrate* is regarded as one essentially broadly triangular in outline and with an anteriorly positioned articulatory facet.

The plesiomorphic condition of the *adductor mandibulae* A_1 muscle in cyprinids would appear an undivided element having its insertion on the outer, posterior portion of the maxilla (as in aspinine cyprinids; see Howes, 1979). Commonly in cyprinids there are two medial sections of the *adductor mandibulae*. The outer (A_2) inserting on the rim of the coronoid process of the dentary, and the inner (A_3) inserting on the coronomeckelian bone (see Takahasi, 1925 : 20). Primitively, the *mentalis* section (A_w) of the adductor complex is present as a well-developed element (as in the bariliines, chelines, aspinines and cultrines) but in the majority of cyprinid taxa it is reduced or lacking entirely (see Takahasi, 1925 : 20).

According to Takahasi (1925) and Matthes (1963) the *protractor hyoideus* (= *genio-hyoideus*) muscle is usually attached to the 1st and/or 2nd branchiostegal rays, rarely to the

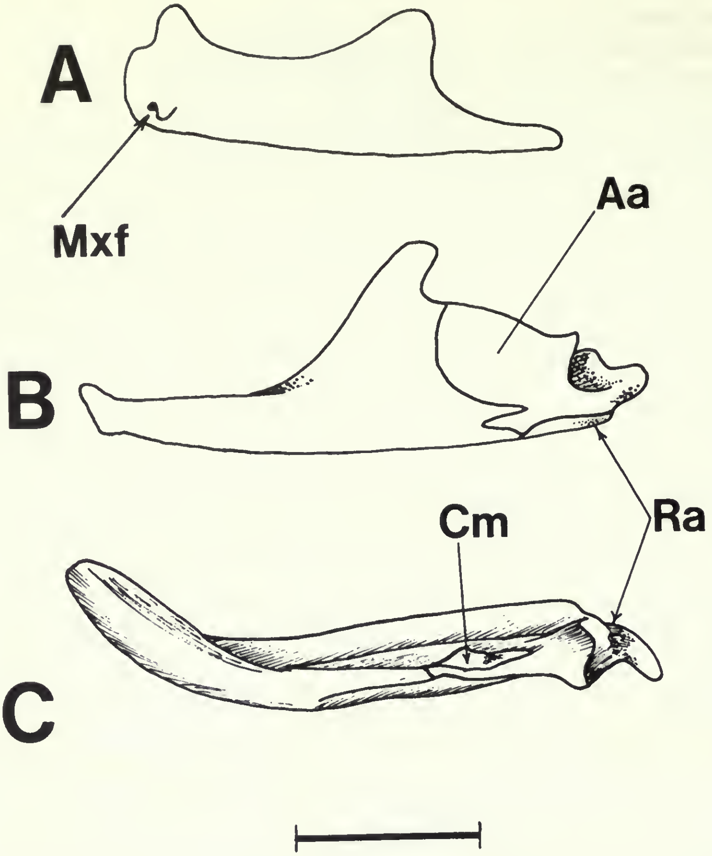

Fig. 10 *Squaliobarbus curriculus*, jaw bones. A, maxilla. B & C, dentary in lateral and dorsal views. Scale = 5 mm.

3rd and never to the interhyal. A tendinous lateral border of the muscle is not uncommon in cyprinids and in many taxa the lateral part of the muscle appears as a separate element.

Semiplotus semiplotus and *S. burmanicus* show markedly derived states of the above hypothesized plesiomorph jaw and muscle morphology. The following features uniquely characterize the jaws of *Semiplotus*:

Upper jaw

1. Premaxilla: shallow, thin, with acute posterior curvature and reduced ascending process.
2. Maxilla: deep, with broad anterior ascending process, reduced mid-lateral process and depressed, notched posterior portion.
3. Bifurcated tendon of muscle A_1 attaching to lateral and medial faces of the maxilla. Some amplification of this character is required. It was noted above that the plesiomorph condition is for muscle A_1 to insert on the outer face of the maxilla. Most often this insertion is tendinous but in bariliine, cheline and aspinine cyprinids it may be musculose across a broad fascia that cover both the dorsal rim of the dentary as well as its lateral aspect (see Howes, 1976 Fig. 23). This, often tendinous, fascia may represent the 'ligamentum primordium' as might the connective tissue in other cyprinids which links the maxilla to the face of the anguloarticular and enwraps the insertion area of the lower jaw musculature. A divided tendinous insertion of the superficial adductor muscle is present in *Cyprinus, Carassius* and *Gobio*. However, unlike the semiplotine

condition, the tendons cross over so that the insertion of the lower element (A_1b) is above that of the upper (A_1a). Takahasi (1925) regarded *Cyprinus* and *Carassius* as representing 'Transitional stages . . .' between the simple bariliine (*Opsariichthys*) and complex gobioine (*Gobio*) types of insertion. Crossing of A_1 tendons also occurs in *Aspidoparia*, a genus with bariliine affinities (see Howes, 1980), *Cosmocheilus, Cyclocheilichthys, Puntioplites* and *Amblyrhynchichthys*. Whilst it is possible that these four latter genera are closely related, such a relationship appears unlikely between them and *Aspidoparia*. All five taxa have a short, deep ethmoid region and the mouth is inferior in position. It is likely that the crossed tendon arrangement is functionally more efficient, in activating jaws of this kind and has been derived independently in the various taxa.

4. Kinethmoid attached to connective tissue overlying the ethmoid bloc.

Lower jaw

5. Dentary: with a sloped labial surface, lateral ridge, outwardly curved coronoid process, ventral posterior process and a synarthritic joint.
6. Anguloarticular rising dorsally to cover the medial face of the dentary coronoid process, only a small portion of the bone extending beyond the posterior border of the dentary; the medial portion extended and formed into stout and complex articular processes.
7. A medial tendon of muscle A_2 to which is attached muscle A_w. Some amplification of this character is required: As noted above, the common, and presumed plesiomorph condition in cyprinids is for muscle A_2 to insert on the rim of the coronoid process of the dentary. In *Semiplotus* and some *Cyprinion* species (see p. 309) the muscle is bifurcated (see above) with both an outer tendinous insertion on the coronoid process and an inner one on the coronomeckelian bone. A segment of muscle stretches from the lower part of the tendon of muscle A_3 to the anguloarticular and should almost certainly be identified as an A_w. Although a similarly developed muscle stems from the tendon of A_3 in *Varicorhinus beso* (p. 317) and some *Barbus* species (Banister, pers. comm.) it does not insert on a medial tendon of A_2 but on the medial face of the anguloarticular.
8. *Protractor hyoideus* muscle connected anteriorly, *via* an aponeurosis, with the *adductor mandibulae* insertions; its posterior part tendinous, attaching to all branchiostegal rays, posterohyal and interhyal.
9. Lateral quadrate facet apposing lateral anguloarticulatory process. Quadrate short and tall.

Comparisons of the jaws in *Semiplotus* with those in *Onychostoma, Varicorhinus, Capoeta* and *Cyprinion*

Taxa with 'sector mouths', i.e. an inferior mouth which is wide and has an exposed cornified mandibular cutting edge; the dentary invariably has a broad, sloping or deflected labial surface, occur frequently amongst the Cyprinidae. Examples are *Onychostoma, Varicorhinus, Capoeta, Cyprinion, Barbus* and some species of *Schizothorax*. Although a cornified lower jaw occurs in *Labeo* and *Garra* it is invariably covered by a thick labial fold.

The jaw morphology of *Onychostoma, Varicorhinus, Capoeta* and *Cyprinion* species is remarkably similar to that of *Semiplotus*. The similarities may be independently derived, i.e. they are convergent, or inherited through a shared common ancester, i.e. they are synapomorphic. These hypotheses are tested by comparative analysis.

Onychostoma laticeps Günther, 1896 (Figs 11A–C)

The *premaxilla* is deeper than that of *Semiplotus* and has no distal ventral curvature, its ventral border is also thick and lacks the sharp, thin edge of the semiplotine bone.

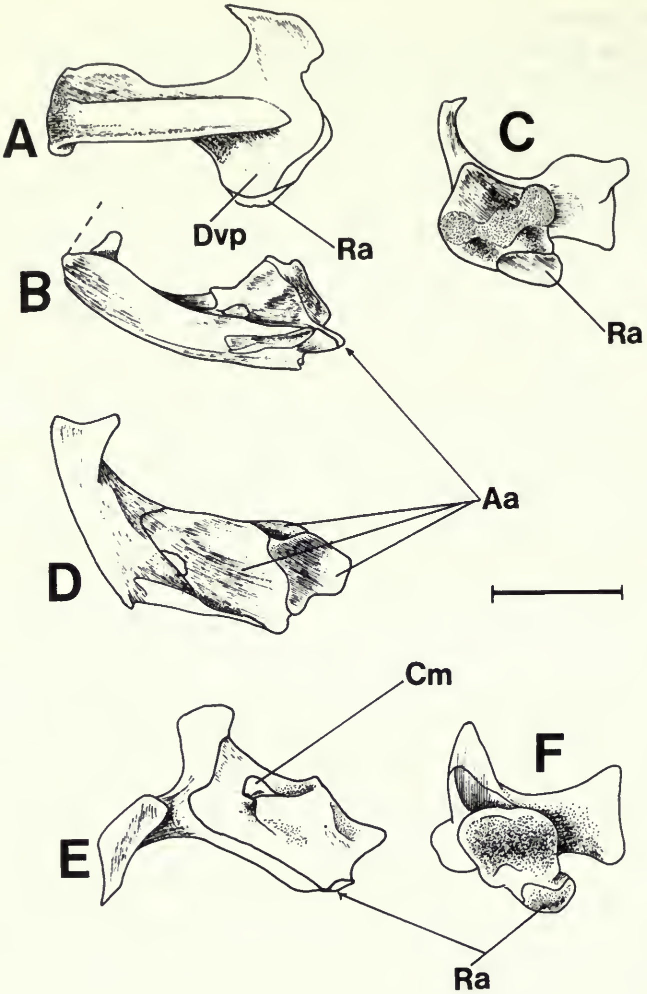

Fig. 11 Lower jaw bones of A, B & C, *Onychostoma laticeps* in lateral, dorsal and posterior views; D, *Varicorhinus beso*, dorsal view; E & F, *Capoeta capoeta* in medial and posterior views. Scale = 5 mm.

The *maxilla* is deep with a broad anterior ascending process. As in *Semiplotus* the mid-lateral process is curved mesially, and although there is a posterior depression of the premaxilla there is no medial notch.

The lower jaw resembles that of *Semiplotus* in a number of features, cf. Figs 5 & 11A. The *dentary* has a bevelled labial surface, a prominent lateral ridge and a postero-ventral process. The coronoid process differs from the semiplotine one and that in other compared taxa in having a markedly concave anterior edge with a long dorso-anterior process. There is no synarthritic joint. The *anguloarticular* is broad, its posterior face shaped into a figure-8 facet. Although the medial portion of the bone forms an articular surface it is not posteriorly extended, nor does it appose a separate facet.

The superficial *jaw musculature* is more complex than in *Semiplotus. Adductor mandibulae* A_1b is extensive, its lower, preopercular part almost entirely tendinous; insertion is *via* a thick tendon to the lateral maxillary face. Muscle A_1a is a parallel fibred element that inserts musculosly on the maxilla above A_1b. The anterior part of the adductor muscle complex is crossed by a band of ligamentous tissue attached dorsally to the inner face of the 1st infraorbital and ventrally to the skin covering the preoperculum (Fig. 12A). Muscle A_2 is a narrow element, its posterior part overlying A_1a (Fig. 12B). The muscle's ventral border is tendinous and insertion is *via* a thick tendon on to the posterior rim of the coronoid process. The area of insertion is invested by a thick connective tissue sheath which extends around the coronoid process and laterally attaches to the maxilla. Muscle A_3 can be distinguished from A_2 by its posterior separation by the *levator arcus palatini* muscle, and its separate insertion onto the coronomeckelian bone.

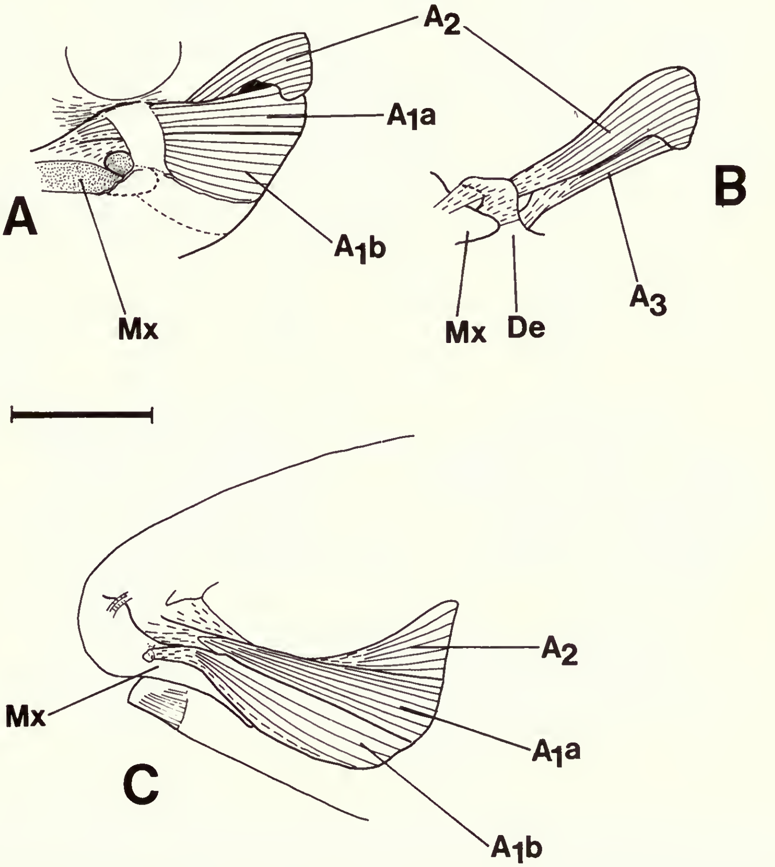

Fig. 12 Jaw musculature of A & B, *Onychostoma laticeps*, A, superfcial and B, deeper muscle layers; C, *Cyprinion microphthalmum* superfcial musculature. Scale = 5 mm.

The *protractor hyoideus* (Fig. 13A) is complex and composed of several sections. The muscle is organised around a tendon that originates from the interoperculum and meets its partner at a median raphe. The anterior part of the muscle runs from the transverse tendon to the inner rim of the dentary. The symphysial area of the muscle grades into a thick, fatty connective tissue which becomes confluent with the lower lip tissue. Laterally, there is a separate segment of the *protractor* running to the hyoid arch. A dorsal portion of the muscle extends from the anterohyal and becomes confluent with the ventral section of the muscle. The posterior body of the *protractor* extends from the branchiostegal rays to the central, transverse tendon; it is dense, with its fibres, or strands of fibres widely separated by a fatty and tendinous tissue. The basal layer of the muscle strongly adheres to the dermis of the hyoid area.

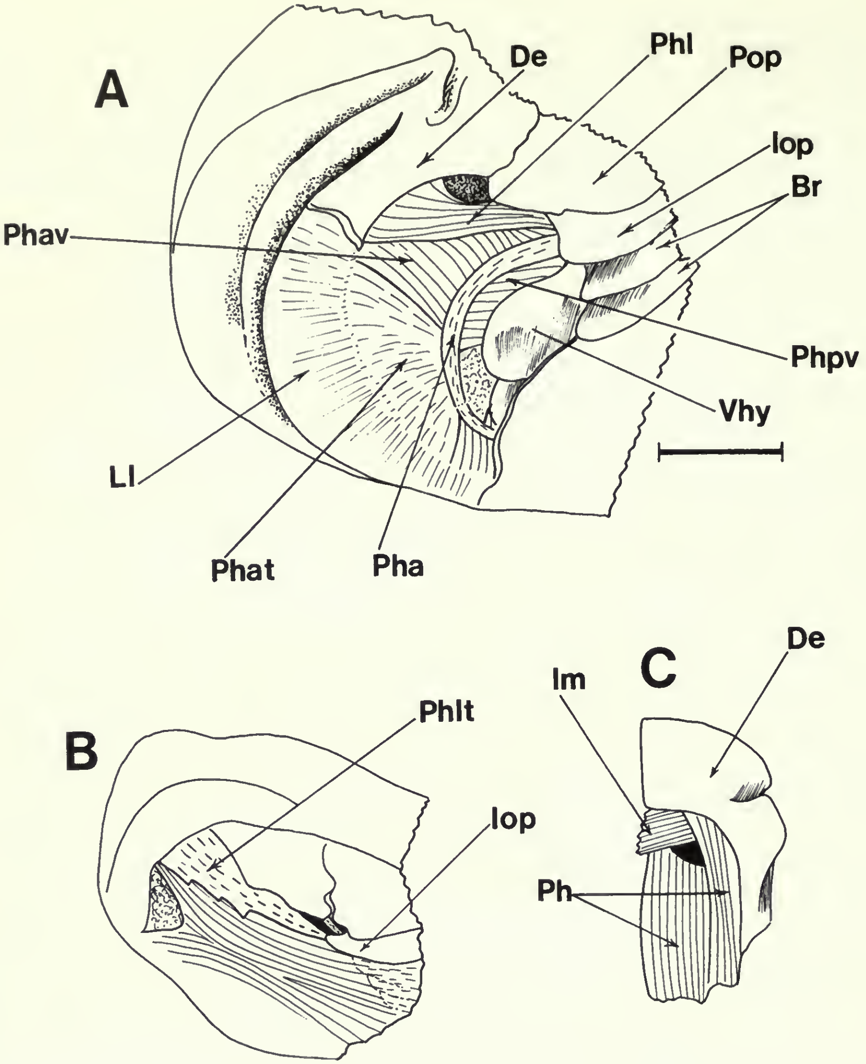

Fig. 13 Hyoid musculature of A, *Onychostoma laticeps* in oblique ventral view. Scale = 10 mm; B, *Varicorhinus beso* in oblique ventral view, and C, *Capoeta capoeta* direct ventral view of left side. B & C are semi-diagrammatic.

The lower lip (Fig. 14)
As in *Semiplotus*, the core of the lip is a deep, broad labial shelf of dense tissue, its dorsal layer (Dls) being of a more fibrous nature. Overlying, and completely free from its dorsal and anterior surfaces is a thick tissue envelope composed of a thin basal layer (Mlt) and a thicker, denser upper layer (Elt) whose lingual portion rises above the dentary rim. Anteriorly the epidermal layer is transformed into a keratinized sheath. Sandwiched between the labial shelf and the basal layer is a thin keratinized band (Mkl) that extends along the central portion of the labial shelf. Ventral to the shelf are layers of tissue which are the counterparts of those lying dorsally. The ventral dermal and epidermal layers (Vmlt, Velt) are, however, firmly attached to the shelf. Unlike *Semiplotus*, there are no tendinous bands connecting the dorsal lip tissue directly with the *protractor hyoideus* muscle and neither, apart from the epidermis, is the ventral tissue contiguous with that muscle.

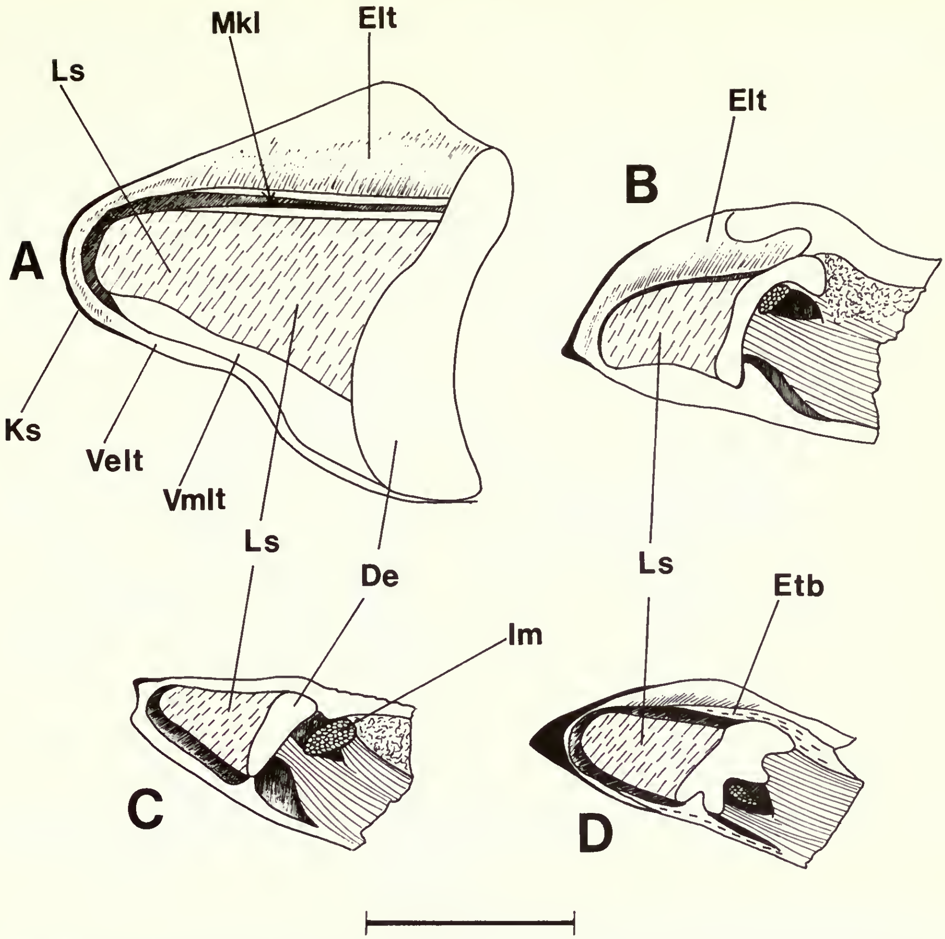

Fig. 14 Sagittal sections through the lower lips of A, *Onychostoma laticeps*; B, *Varicorhinus beso*; C, *Capoeta capoeta*; D, *Cyprinion macrostomum*. Scale = 10 mm.

Varicorhinus beso Ruppell, 1836

The *premaxilla* is shallow and lacks a prominent anterior ascending process; the *maxilla* has broad and thick anterior, and long, mesially curved mid-lateral processes. Unlike *Semiplotus*, the posterior portion of the maxilla is not expanded, compressed or medially notched.

The *dentary* (Fig. 11D) has an abrupt mesial curvature with a broad labial surface and a laterally protruding process at the rictus; its coronoid process is tall and slopes outward. The *anguloarticular* is short and broad, its anterior tip extending beyond the base of the coronoid process. Unlike *Semiplotus* the articular facet is not developed into medial processes, and it is transversly aligned.

The *quadrate*, like that in *Semiplotus*, is short and deep with an expanded articulatory facet. The facet is a double ellipsoid inclined at 45° to the transverse horizontal. In contrast to *Semiplotus* the facet is confined to the anterior face of the bone, no part extending to the lateral surface.

The jaw musculature differs from *Semiplotus* in that *adductor mandibulae* muscle A_1 has a single tendinous insertion on the maxillary outer face. A small A_w portion fans out from the tendon of A_3 across the anguloarticular and part of the coronoid process. The *protractor hyoideus* is strongly developed, its main portion attaching tendinously to the 1st and 2nd branchiostegal rays and to the posterohyal (Fig. 13B). A lateral part attaches *via* a strong tendon (almost ossifed in large specimens) to the anterior tip of the interoperculum, a feature not found in *Semiplotus*. Its anterior part becomes tendinous and fans out to attach along the posterior rim of the dentary (Fig. 13B).

The *lower lip*, although having the same basic structure as in *Semiplotus* has a less complex histological structure (Fig. 14B). The differences are a shallower labial shelf, lack of a basal dermal tissue layer, the dermis united at its central portion with the labial shelf, and more extensive keratinization of the anterior epidermis. There are no tendinous connections between the lip tissue and the *protractor hyoideus* muscle.

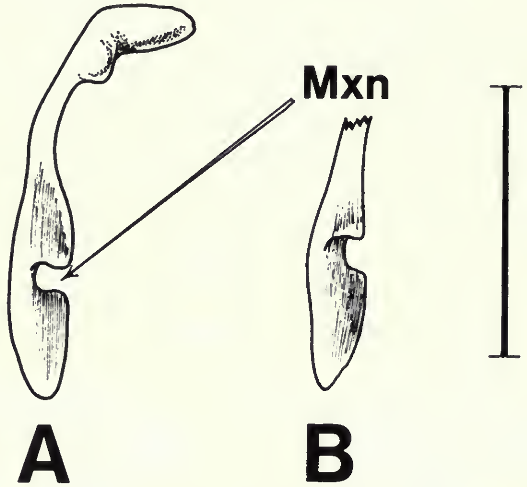

Fig. 15 Premaxillae in dorsal view of A, *Cyprinion watsoni*; B, *Capoeta capoeta* posterior portion only. Scale = 5 mm.

Capoeta capoeta Guldenstadt, 1773

The *premaxilla* lacks an anterior ascending process; the *maxilla* has a marked mesial curvature, a thick and wide anterior and a shallow mid-lateral ascending process. The posterior arm of the maxilla, as in *Semiplotus*, is compressed and medially notched (Fig 15).

The *dentary* has the same abrupt medial curvature and antero-ventrally sloped labial surface as in *Varicorhinus beso* (Fig. 11E). Unlike *Semiplotus, Onychostoma* and *Varicorhinus*, the coronoid process is aligned at 45° to the midline, so that it is set at the curve of the dentary. The ventro-posterior surface of the dentary is broad, as is the depressed anguloarticular which overlies it. The articulatory facet is ovate and transversly aligned (Fig. 11F).

The jaw musculature of *Capoeta* is similar to that of *Semiplotus* and *Varicorhinus*. *Adductor mandibulae* A_1 is a single muscle with a central anterior aponeurosis; insertion is *via* a thick tendon onto a lateral maxillary process. A thin tendinous strip of tissue runs from the dorso-anterior part of the muscle to insert on the connective tissue covering the medial face of the maxilla. Muscle A_2 inserts entirely on the posterior border of the dentary coronoid process; a separate group of fibres leaves the main tendon to run ventrally across the medial coronoid face. Tendon A_3 inserts on the coronomeckelian bone.

The *protractor hyoideus* is extensively tendinous in its posterior part and it is attached to all the hyoid elements except the interhyal. There is no lateral portion stemming from the interoperculum as in *Varicorhinus*. Anteriorly the left and right arms of the muscle are widely separated so that the *intermandibularis* is exposed (Fig. 13C).

The *lower lip* differs from that in the other taxa compared here in having a narrow labial shelf, no layered organisation of the tissue overlying the shelf, and this tissue continuous with that lining the mouth. The outer, keratinized sheath lies along the upper edge of the labial shelf rather than around its anterior face.

Cyprinion Heckel, 1843

In *Cyprinion* species, the *premaxilla* usually lacks an ascending process, and when one is present it is but slightly developed. Maxillary shape is interspecifically variable and in only one species, *C. watsoni*, does it closely resemble *Semiplotus* in having a reduced, medially directed mid-lateral ascending process and a depressed, medially notched posterior arm (Fig. 15).

The lower jaw of *C. macrostomum* and *C. microphthalmum* resembles that of *Semiplotus* more closely than does that of any other *Cyprinion* species. This resemblance is in the

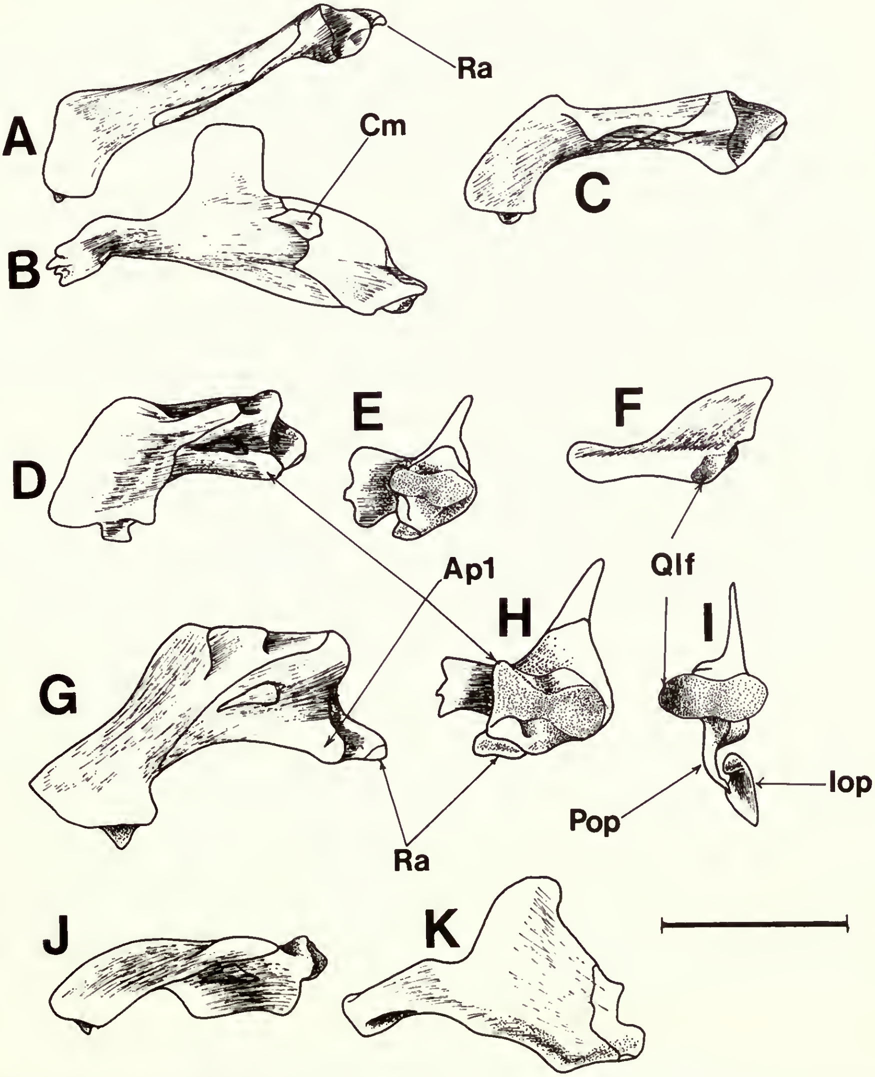

Fig. 16 Lower jaw bones (right side) of A & B, *Cyprinion acinaces* in dorsal and medial views; C, *Cyprinion watsoni* in dorsal view; D & E, *Cyprinion microphthalmum* in dorsal and posterior views; F, quadrate in lateral view; G & H, *Cyprinion macrostomum* in dorsal and posterior views; I, quadrate in anterior view; J & K *Cyprinion kais* in dorsal (right jaw bone) and lateral (left jaw bone) views. Scale = 5 mm.

curvature of the dentary, a complex synarthritic joint and the broad articular surface of the anguloarticular. There is a slight medial process, equivalent to process Ap1 in *Semiplotus*, separated from the lateral part of the bone by a deep cleft. Both *Cyprinion* species also possess a quadrate bearing part of its articulatory facet laterally (Fig. 16F). *Cyprinion watsoni* has a more elongate jaw than *C. microphthalmum* and *C. macrostomum*, but the anguloarticular has a similar broadening of its facet.

With the exception of *C. microphthalmum* the muscles attaching to the upper jaw are undivided or only partially divided. In that species the *adductor mandibulae* A_1a is separated from A_1b for almost its entire length but shares a common insertion with it on both the outer and inner aspects of the maxilla (Fig. 12C). The lower jaw muscles are also interspecifically variable with respect to their proportions and fibre orientation, but their insertions are essentially similar. There is some variability in the size of muscle A_w. In *C. microphthalmum* and *C. macrostoma*, as in *Semiplotus* it inserts on a medial tendon of muscle A_2.

The lower jaws of *C. acinaces, C. milesi* and *C. watsoni* are less derived with respect to their labial and articulatory surfaces but all have a synarthritic joint of varying complexity, the weakest being in *C. acinaces* (Fig. 16A). The jaw of *C. acinaces* is regarded as the most plesiomorph of all *Cyprinion* species with respect to its moderately expanded labial surface, mid-laterally placed coronoid process and small, transverse articulatory facet. The lower jaw of *C. kais* is deeper posteriorly than in any other *Cyprinion* species, and its labial surface is much narrower (Fig. 16J); as in *Semiplotus*, the anguloarticular covers a substantial area of the medial face of the dentary coronoid process. In all *Cyprinion* species, the anguloarticular extends posteriorly only marginally beyond the dentary.

The lower lip of *Cyprinion* is of the same layered type found in *Semiplotus* (Fig. 14D), with that of *C. macrostoma* having the greatest resemblance in terms of dimensions of the labial shelf, tissue layering, and tendinous connections with the *protractor hyoideus* muscles. The degree of keratinization is interspecifically variable but reaches its greatest development in *C. macrostomum*.

Onychostoma, Varicorhinus and *Capoeta* all lack the *Semiplotus* features of a synarthritic mandibular joint, medial anguloarticular processes, lateral quadrate facet, aponeurotic connection of the *adductor mandibulae* and *protractor hyoideus* muscles, interhyal connection of the *protractor hyoideus*, and complexity of lower lip structure. *Onychostoma* shares with *Semiplotus* a lateral dentary ridge and posteroventral process, but the nature of the coronoid process and the lack of the apomorphies cited above favour the hypothesis that the derived jaw characters held in common have been independently acquired. Likewise, the sector type of mouth morphology of *Varicorhinus* and *Capoeta* is believed to be a convergent feature.

The phyletic relationships of *Onychostoma, Varicorhinus* and *Capoeta* have yet to be determined, but other apomorphies (absent in *Semiplotus* and *Cyprinion*) suggest the following affinities: *Onychostoma* is related to *Ageniogarra* and possibly to a group of Chinese '*Schizothorax*'; *Varicorhinus* forms a close relationship with certain African *Barbus* (Banister, in preparation); *Capoeta* is the likely sister-group to *Cyprinus* and *Carassius* (see Howes, 1981).

As noted above all *Cyprinion* species possess a synarthritic mandibular joint, aponeurotic connection of the *adductor mandibulae* and *protractor hyoideus* muscles and similarly developed lower lip structure. Synapomorphies other than those of the jaws also suggest a close relationship between *Semiplotus* and *Cyprinion*.

Other apomorph characters of *Semiplotus*

In addition to the jaws, *Semiplotus* species are characterized by other and presumed apomorphic features.

1. *Condylar articulation of the interhyal with the symplectic.* The usual condition in cyprinids is for the symplectic to be an elongate bone. It is rarely short and deep, and

only in a minority of taxa is the posterior face concave and in articulation with the interhyal. The common condition of the interhyal is a lamellate bone, sometimes incompletely ossified.

In *Semiplotus* the symplectic is short and buttress-like (Figs 6 & 17A), its posterior surface is concave and articulates directly with the interhyal, thereby forming part of the ball and socket joint between the two elements. The interhyal is short and cylindrical, and articulates with the dorsal surface of the posterohyal *via* a cartilaginous meniscus.

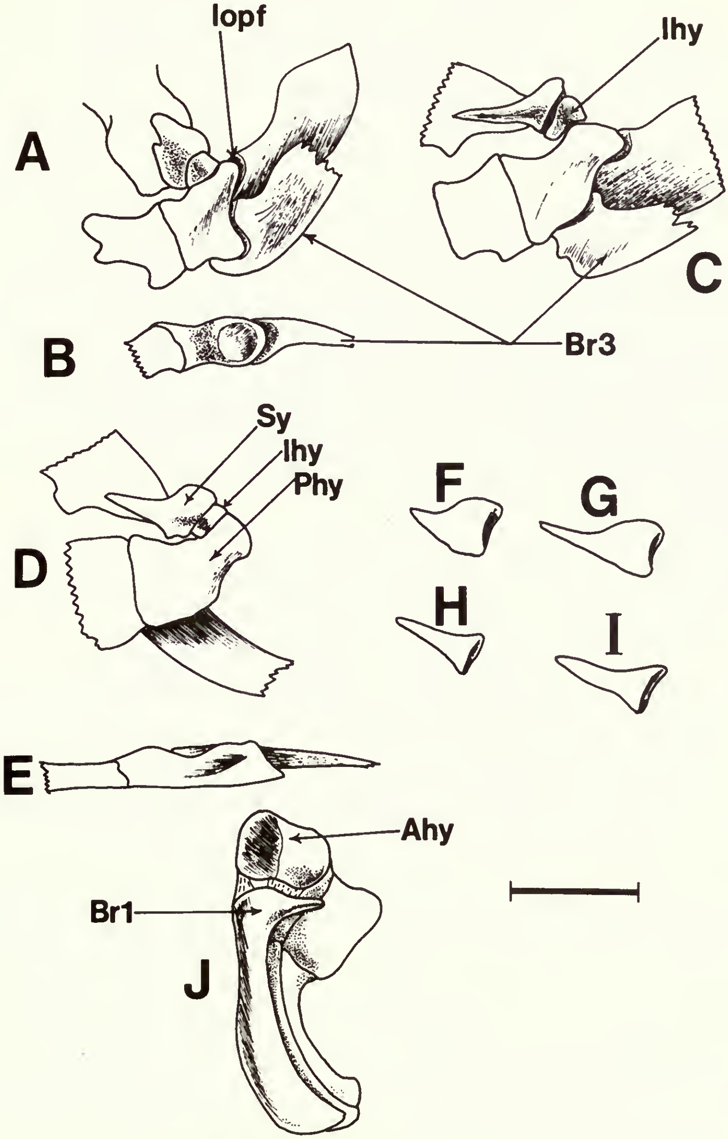

Fig. 17 Hyoid and suspensorial elements of A & B, *Semiplotus semiplotus*, medial and dorsal views of posterior hyoid bar; C, *Cyprinion macrostomum*, medial view of posterior hyoid bar; D & E, *Varicorhinus beso*, medial and dorsal views of posterior hyoid bar; F–I, symplectic bones of F, *Cyprinion microphthlamum*; G, *C. kais*; H, *C. acinaces*; I, *C. watsoni*; J, *Cyprinion kais*, anterior view of 1st branchiostegal ray and hyoid bar. Scale = 3 mm.

Amongst the taxa considered here, only in *Onychostoma* and some species of *Cyprinion* does the symplectic approach that of *Semiplotus* in size and shape. In *Onychostoma*, the condylar surface of the bone faces ventrally whereas in *Semiplotus* and *Cyprinion* it is angled postero-ventrally. The interhyal in all these genera, and in *Varicorhinus*, is hypertrophied and articulates with the dorsal aspect of the posterohyal, but since there are no other synapomorphies of the hyoid elements shared by *Onychostoma, Varicorhinus* and *Semiplotus*, these are considered to be independently derived features (see p. 320).

2. *Ventral and lateral articulation of the 3rd branchiostegal ray with the posterohyal* (Figs 17A & B). Plesiomorphically the 3rd branchiostegal is attached ligamentously to the lateral face of the posterohyal. In *Semiplotus*, the posterohyal is short and thick, and the branchiostegal ray expanded medially so as to form a shelf underlying the ventral border of the posterohyal with whose posterior portion it articulates. The anterior part of the branchiostegal shelf is attached ligamentously to the medial face of the posterohyal whilst the proximal lamellate area of the branchiostegal ray is attached to the lateral face of the hyal.

   A slight medial shelf is present on the 3rd branchiostegal rays of *Varicorhinus* and *Capoeta*. It is, however, barely developed in these taxa and the posterohyal is not distally expanded as in *Semiplotus* (Fig. 17). Such an expansion of the branchiostegal is lacking in *Onychostoma*. Only in *Cyprinion* is there a substantial 3rd branchiostegal shelf, which in *C. macrostomum* is developed much as in *Semiplotus* (Fig. 17).
3. *Ventrally directed supraethmoid and hypertrophied vomer* (Figs 18A–C). Although the rostral curvature of the ethmoid bloc is variable in the Cyprinidae (see Howes, 1980) nowhere is it more extreme than in *Semiplotus* where the supraethmoid is almost vertically aligned. An apparent correlate of this condition is the hypertrophied vomer, whose enlargement also results in a steep angle forming between it and the parasphenoid (Fig. 18A).

   In both *Onychostoma* and *Varicorhinus* the ethmoid is strongly curved ventrally and there is a corresponding hypertrophy of the vomer. In these genera the ventrally directed part of the supraethmoid is confined to the lower part of the bone. In *Cyprinion macrostomum* the curvature of the supraethmoid more closely resembles the condition in *Semiplotus* where the entire bone slopes ventrally.
4. *Frontal-supraethmoid foramen* (Figs 18B–C). Synapomorphic for *Semiplotus semiplotus* and *S. burmanicus* is a foramen between the frontals and the supraethmoid (see p. 304). The posterior border of the foramen indents each frontal to form a notch in much the same way as the antero-medial supraethmoid notch occurs in other cyprinids. Likewise, the frontal notch of *Semiplotus* performs a similar function, namely in providing a hold-fast for the kinethmoid ligaments. Attachment of kinethmoid ligaments to the frontal instead of the supraethmoid is unknown in any other cyprinid.
5. *Elliptical subtemporal fossa with major contribution from the pterotic* (Fig. 18D). The plesiomorph subtemporal fossa is shallow with a round or oval outline (see Howes, 1981). In *Semiplotus* the fossa is deep and markedly ellipsoidal, its long axis transverse. Only in *Onychostoma* does the subtemporal fossa approach the shape of that in *S. semiplotus* and *S. burmanicus*, but it lacks the extreme depth of those species.

   Typically the posterior wall of the subtemporal fossa in cyprinids is formed principally by the exoccipital, with a minor contribution from the pterotic (see, for example, Howes, 1978, Figs 6 & 33; 1980, Fig. 13). In *Semiplotus* the greater part of the posterior wall is formed by the pterotic (Fig. 18D); only in *Cyprinion* is there a similarly substantial contribution of the pterotic.
6. *Proximal part of supraoccipital crest formed by the parietals* (Fig. 19A).
   Semiplotus species have a high supraoccipital crest; the parietals are short and slope upwards, their medial portions extending posteriorly and embracing the base of the supraocipital crest. With the exception of *Cyprinion*, in no other cyprinid taxon, even

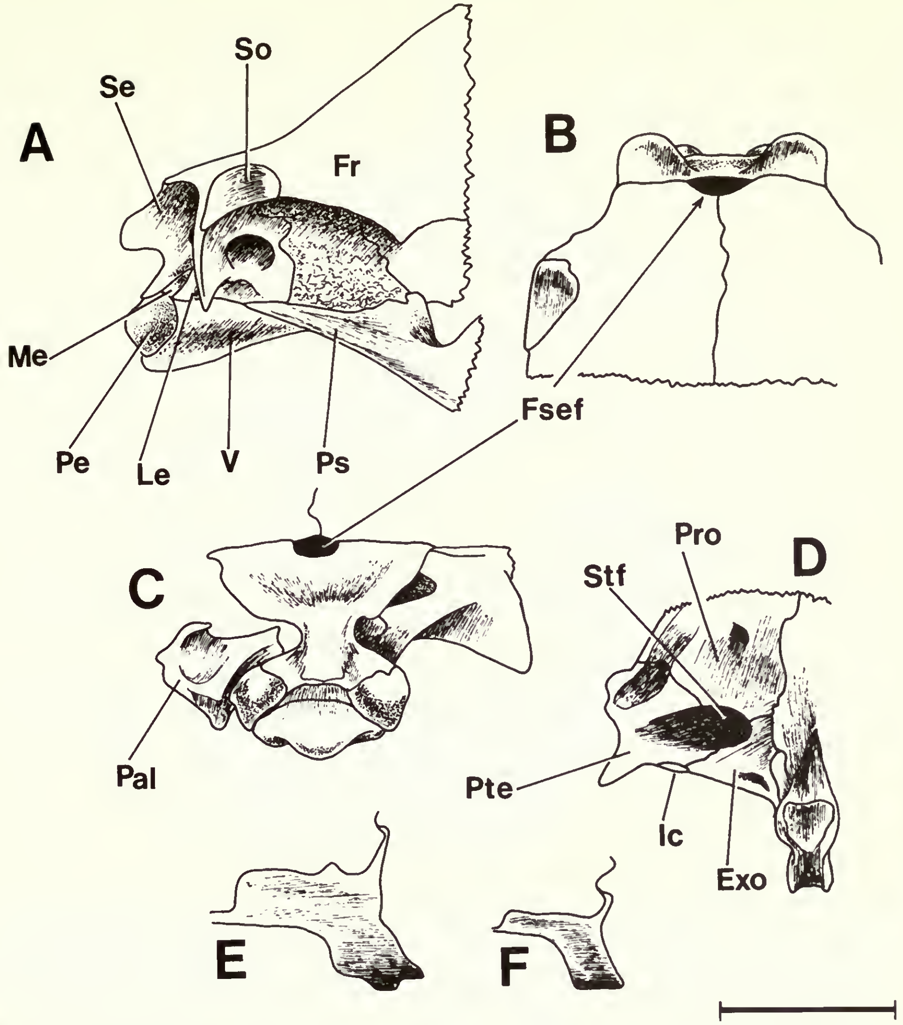

Fig. 18 *Semiplotus semiplotus*, cranium. A, lateral view of ethmo-vomerine and orbital areas; B, dorsal & C, anterior views of ethmoid region; D, ventral view of posterior cranial area; E & F, basioccipital process in lateral view of E, *S. semiplotus* and F, *S. burmanicus*. Scale = 10 mm.

those with a relatively high supraoccipital crest, does the parietal extend postero-medially. In *Cyprinion* there is some variability in the length of the parietal, but in all species it extends postero-medially to form part of the supraoccipital crest (Figs 19B–C).

7. *Reduced basioccipital process and masticatory plate* (Figs 18E & F).
Although a reduction of the basioccipital process and masticatory plate occurs in several groups of cyprinids (see Howes, 1981), in none is the reduction so extreme as in *Semiplotus*. In *S. burmanicus*, the basioccipital (masticatory) plate is entirely absent and the ventral (aortic) ossification is transversly convex. Only in some *Cyprinion* species (*C. kais* and *C. microphthalmum*) is a truncated basioccipital process associated with marked reduction of the ventral plate.
8. *Interoperculum-preoperculum articulation* (Figs. 6B–C).
In *Semiplotus* the anterior tip of the preoperculum is formed into a condyle and is curved medially so as to overlie the anterodorsal part of the interoperculum; the

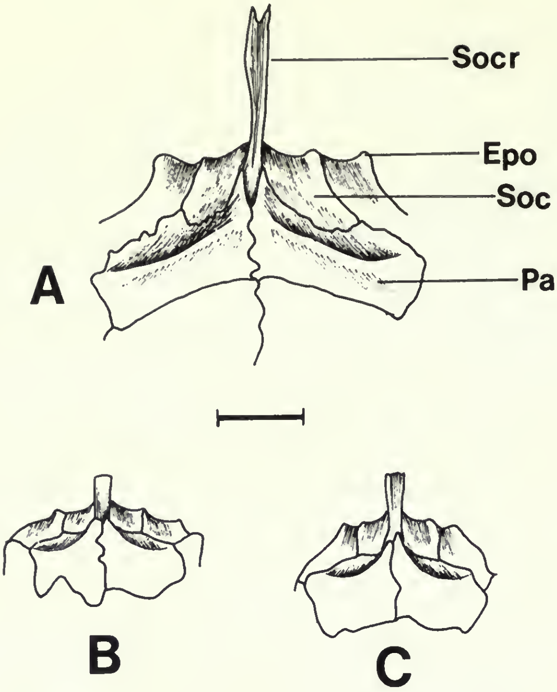

Fig. 19 Dorsal posterior cranium of A, *Semiplotus semiplotus*; B, *Cyprinion macrostomum*; C, *Cyprinion kais*. Scale = 5 mm.

anterior tip of the interoperculum is formed into a facet. The two elements are firmly articulated and the medial curvature of the preoperculum beneath the quadrate appears to reinforce the rigidity of the quadrate-lower jaw articulation. The interoperculum also bears a medial facet with which the rounded tip of the posterohyal articulates.

In *Varicorhinus* there is a similar development of the terminal point of the interoperculum, but only in *Cyprinion* do both elements articulate as in *Semiplotus* (Fig. 16I). A medial interopercular facet is variously developed in the Cyprinidae, but in *Cyprinion* alone is it of similar depth and position.

9. *Development of the supraneurals and articulation with 1st dorsal pterygiophore* (Fig. 20). The supraneurals of *Semiplotus* are hypertrophied and each is in contact with its respective neural spine. The 'neural complex' of the Weberian apparatus is upright and has an almost straight anterior edge; dorsally it contacts the posteriorly directed supraoccipital process. This is contrary to the usual cyprinid condition where the anterior border of the neural complex is concave, giving it an axe-shaped appearance. In *Semiplotus semiplotus* there are 5 or 6 supraneurals, each articulating with its neighbour; the posterior element is bifurcated and overlaps the anterior margin of the 1st dorsal pterygiophore. *Semiplotus burmanicus* has 7 supraneurals, all somewhat thinner than in *S. semiplotus* but similarly and sequentially joined, each bearing a vertical ridge laterally. The 1st supraneural is narrowly separated from the neural complex.

Although enlarged supraneurals occur in other cyprinid taxa they are never so tall as those in *Semiplotus semiplotus*. Apart from *S. burmanicus*, interlocking of the last supraneural with the 1st pterygiophore occurs only in *Cyprinion macrostomum*, and a straight-edged neural complex is shared only with *Cyprinion microphthalmum*.

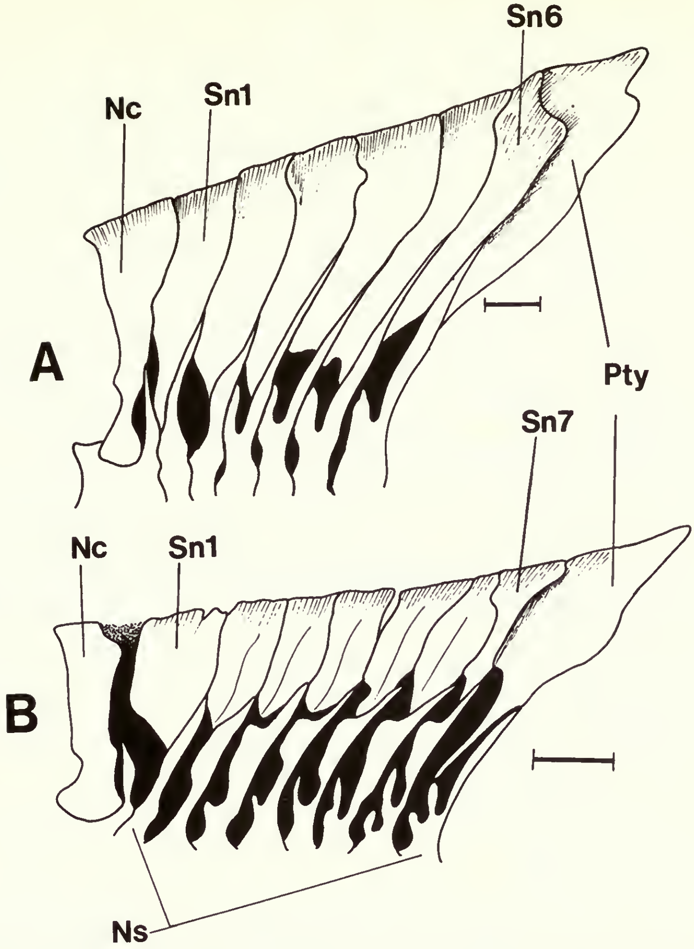

Fig. 20 Anterior vertebral column of A, *Semiplotus semiplotus*; B, *S. burmanicus*. Scale = 5 mm.

The relationship between *Semiplotus* and *Cyprinion*

In addition to the jaw synapomorphies (p. 320), *Semiplotus* shares with *Cyprinion* species a series of derived hyoid, cranial and vertebral features (enumerated above as 1–9), some of which are present in all *Cyprinion* (1, 2, 5, 6, 8), others in only some species of that genus (3, 7, 9).

At present, the genus *Cyprinion* cannot be defined on the basis of even a single autapomorphy. Derived characters such as the expansion of the proximal portion of the pelvic fin rays, interpelvic papillate flaps (see Banister & Clarke, 1977) and a naked pre-dorsal ridge (see Mirza, 1969) although synapomorphic for some species do not occur in all members of the genus. If, however, the concept of *Cyprinion* is expanded so as to include *Semiplotus*, then the taxon so formed is recognisable as a monophyletic unit on the basis of several synapomorphies (the principal one being the presence of a synarthritic dentary joint), and the problem posed by those apomorphies shared by *Semiplotus* and some *Cyprinion* species is also overcome. Thus (following Heckel, 1843; see p. 331), *Semiplotus* is regarded as a junior synonym of *Cyprinion* and any references to *Cyprinion* from here onwards must be taken to include *Semiplotus semiplotus* and *S. burmanicus*. (A synopsis of included taxa is given on p. 331.)

Discussion

Apomorph character distribution in *Cyprinion* species

If the jaws of *Cyprinion semiplotum* are seen as the terminal stage of increasing complexity, then there is a possibility that an evolutionary or 'transitional sequence' of jaw types might reflect the pattern of interspecific relationships within the genus *Cyprinion*. However, such an arrangement of increasingly derived jaw morphology (in terms of hypertrophy or reduction of various elements) is not congruent with polarized morphoclines in other characters amongst *Cyprinion* species.

Jaw synapomorphies possessed by *C. semiplotum* and *C. burmanica* unite them with other *Cyprinion* species in the following patterns:

(i) A greatly increased complexity of the mandibular synarthritic joint, a broad anguloarticular with a medial process and a cleft between the lateral and medial faces of the bone. Shared with *C. macrostomum, C. microphthalmum* and *C. watsoni.*

(ii) A lateral quadrate facet and a medial A_2 tendon. Shared with *C. macrostomum* and *C. microphthalmum.*

(iii) A medial maxillary notch. Shared with *C. watsoni.*

(iv) A divided insertion of *adductor mandibulae* A_1 muscle. Shared with *C. microphthalmum.*

Any 'transitional series' present amongst this character complex is interrupted by the distribution of characters (iii) and (iv). The following synapomorphies uniting *C. semiplotum* and *C. burmanica* among other *Cyprinion* species display incongruent patterns when set against those of the jaw:

(v) A deep symplectic and a truncated basioccipital process with a reduced masticatory plate. Shared with *C. kais* and *C. microphthalmum.*

(vi) A straight-edged neural complex. Shared with *C. microphthalmum.*

(vii) Articulation of the last supraneural with the 1st pterygiophore.
Shared with *C. macrostomum.*
Synapomorphies which are not present in *C. semiplotum* and *C. burmanica* unite the following species:

(viii) 1st branchiostegal ray articulating ventrally with the ceratohyal through a long medial process (Fig. 17). Shared only by *C. macrostomum* and *C. kais.* (*Cyprinion kais*, it should be remembered has neither of the derived jaw characters (i) nor (ii) which *C. macrostomum* shares with other species).

(ix) Pelvic flaps and papillate interpelvic region. Shared by *C. watsoni, C. acinaces* and *C. milesi.* The two latter species are conservative in their cranial and jaw morphologies (see p. 320) and are thought to comprise the plesiomorph lineage within the genus. Thus, unlike *C. watsoni, C. acinaces* and *C. milesi* share none of those characters that distinguish the more derived lineage (see (i) and (ii) above).

In virtually all monophyletic assemblages of cyprinid fishes so far identified there are sets of incongruent apomorphies, a state of affairs which makes it impossible to apply a rigidly dichotomous system of relationships. Such incongruencies usually can be ascribed to some form of homoplasy, particularly when the characters in question occur in outgroups, as for example the medial maxillary notch present in *Cyprinion semiplotum, C. burmanica, C. watsoni* and also in *Capoeta*. Here the most likely explanation for its presence in *Capoeta* and *Cyprinion* is one of parallelism as no other synapomorphies unite *Capoeta* with *Cyprinion*; see p. 320. However, its distribution within the three *Cyprinion* species can only be accounted for most parsimoniously by assuming its loss in two other species (*C. microphthalmum* and *C. macrostomum*).

Other character sets also reveal incongruency when treated dichotomously. For example, in *Cyprinion kais* one must postulate the loss of all jaw synapomorphies plus the parallel evolution in this species and in *C. semiplotum, C. burmanica* and *C. microphthlamum* of similarly derived symplectic and basioccipital characters. Furthermore, the loss of a supraneural-pterygiophore articulation must be assumed in *C. kais* and *C. microphthalmum*, and interpelvic papillate flaps must be treated either as a plesiomorph character or assumed to be secondarily derived in *C. watsoni*. Such solutions result in a confusing mixture of assumed parallelism and reversal, with the acceptance of one alternative being no more parsimonious than the acceptance of another; see cladogram, Fig. 21.

Bremer & Wanntorp (1979) have discussed the difficulties posed by conflicting synapomorphies and show that the situation may best be displayed as reticulate cladograms. Such a device is used here to show character distribution in *Cyprinion* (Fig. 22).

Although sister species cannot be identified with this synapomorphy scheme, both apomorph character weighting and the simplistic, essentially numerical approach of using

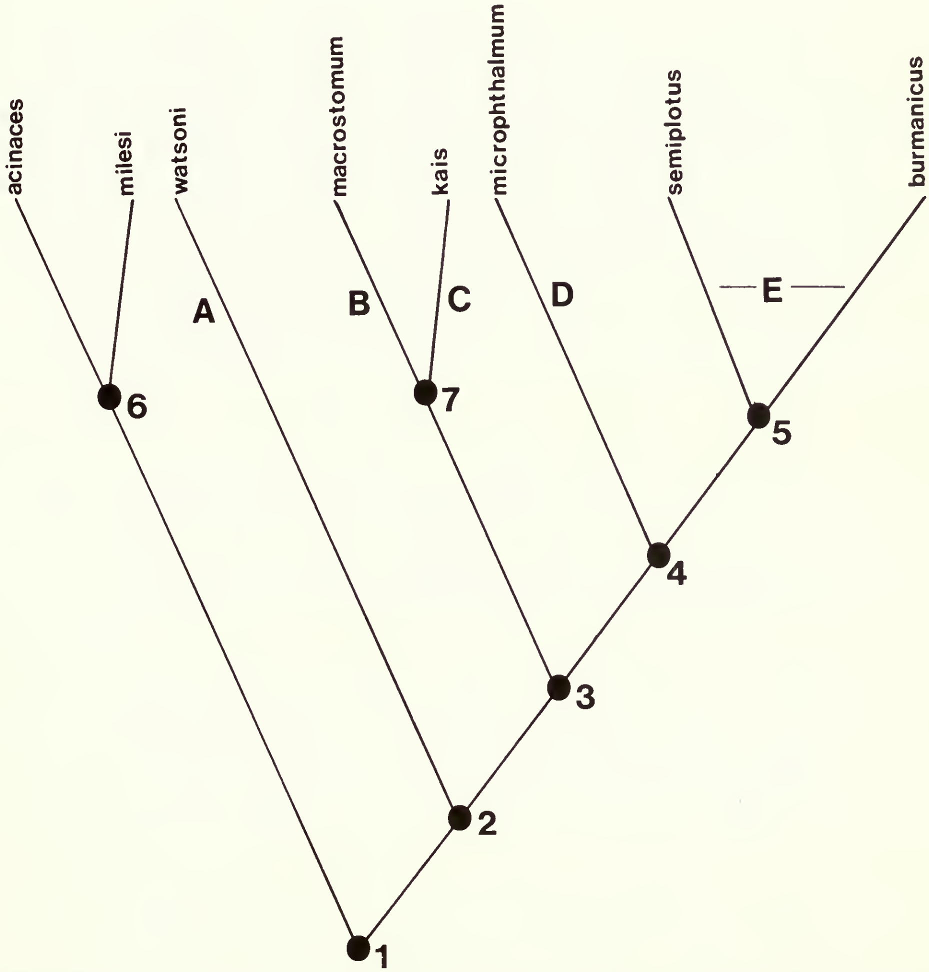

Fig. 21 Most parsimonious cladogram of *Cyprinion* characters. *Synapomorphies*; nodes 1, *Cyprinion* synapomorphies (including expanded pelvic fin rays); 2, jaw synapomorphies (see text, p. 320); 3, lateral quadrate facet, medial A_2 tendon, truncated basioccipital, deep symplectic; 4, upright neural complex; 5, jaw and cranial synapomorphies (see text); 6, interpelvic papillate flaps; 7, method of articulation of 1st branchiostegal with ceratohyal (see text, p. 326). *Parallelisms and reversals*; lineage A, scaleless interpelvic region (parallel to 6); B, loss of deep symplectic and truncated basioccipital in *C. macrostomum*, parallelism of pterygiophore-supraneural articulation to *C. semiplotus* and *C. burmanicus*; C, loss of jaw synapomorphies in *C. kais*; D, loss of supraneural-pterygiophore articulation in *C. microphthalmum*; E, loss of pelvic fin ray expansion in *C. semiplotus* and *C. burmanicus*.

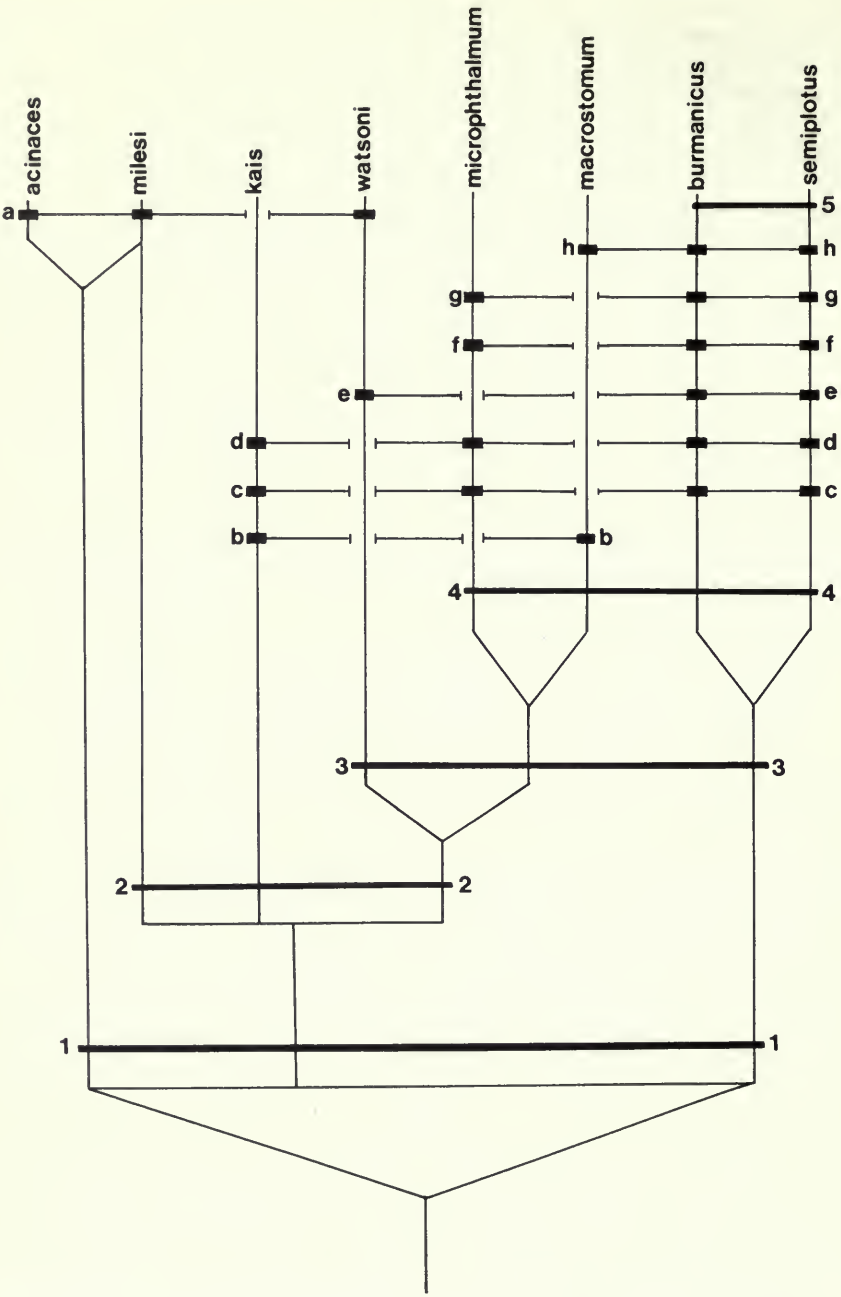
acinaces
milesi
kais
watsoni
microphthalmum
macrostomum
burmanicus
semiplotus
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Fig. 22 Reticulate synapomorphy scheme for *Cyprinion* characters Level 1, *Cyprinion* synapomorphies (see text, p. 325); 2, expanded pelvic fin rays; 3, increased complexity of synarthritic joint, broadened anguloarticular with medial process Ap_3; 4, lateral quadrate facet, medial A_2 tendon, interopercular-preopercular articulation; 5, jaw and cranial synapomorphies (see text, p. 312). *Conflicting synapomorphies*: (*a*) interpelvic papillate flaps; (*b*) articulation of 1st branchiostegal ray; (*c*) upright neural complex; (*d*) divided *adductor mandibulae* A_1; (*e*) medial maxillary notch; (*h*) supraneural–pterygiophore articulation. Black boxes indicate the presence of that character on a particular lineage, a break in the horizontal indicates its absence.

the greatest number of synapomorphies as an assessment of relationship is avoided (Tarsitano & Hecht, 1980: 178). Likewise, the alternative approach, using unresolved polychotomies, serves only to indicate that there is an absence of characters rather than the presence of conflicting ones.

It may be argued that the choice of character sets employed here is itself a weighting procedure, and that the use of other sets would reveal dichotomous sister-group relationships. The counterclaim to these arguments is that the characters employed are those whose intraspecific variability is known, and indeed are the only definitive characters recognizable at this level of investigation. Cyprinids are 'notorious' for their conservative characters (see for example Regan, 1911). Banister (1980) held that this conservatism '... coupled with the occasional small saltatory morphological changes ... has the effect of making it difficult, if not impossible to distinguish between parallelism and the sharing of characters derived through common ancestry'. In each of the cyprinid groups so far identified as monphyletic (the aspinines, chelines, bariliines and abramines) one lineage appears as the bearer of a large number of autapomorphies and thus leaves a considerable 'morphological gap' between it and the more conservative corpus of lineages comprising that particular group. Examples are *Macrochirichthys* + other chelines and *Hypophthalmichthys* + other abramines (see Howes, 1979; 1981). Such also appears to be the case within *Cyprinion* where *C. semiplotum* and *C. burmanica* represent a highly derived lineage characterized by many jaw synapomorphies. Presumably the accumulation of synapomorphies in one such lineage is the result of a cumulative series of speciation events, lacking in the other, more generalized lineages (i.e. 'the occasional small saltatory changes' of Banister, 1980).

Whether the reticulate pattern of relationships is an artifact resulting from incomplete character analysis or a reflection of polymorphic descent through populations of the intragroup lineages is a problem as yet unresolved.

Evolution of the *Cyprinion* jaw and the 'sector mouth'

Even though no 'transitional series' of jaw types emerges from the reticulate pattern presented (Fig. 22), particular synapomorphies indicate a possible evolutionary course leading to the specialized morphology of the *Cyprinion semiplotum*-*C. burmanica* lineage. Comparison of these apomorphies with similar but independently derived characters in other cyprinid lineages indicates those features which are prerequisites for the development of a sector mouth.

In the upper jaw a decisive step towards a sector mouth appears to have been taken with the reduction of the premaxillary ascending process. Matthes (1963) remarks that reduction of this process probably occurred independently in several genera and is not therefore indicative of close relationship. Matthes was referring particularly to similarities between *Varicorhinus, Labeo* and *Garra.* Whilst this study endorses Matthes' view that this particular feature is not necessarily a synapomorphy for all three genera, it does not refute its possible synapomorphic status in *Labeo* and *Garra*, which share other derived characters (Reid, unpublished thesis).

At first sight it would seem that reduction of the premaxillary processes should lead to restricted protrusibility of the upper jaw. However, this may be compensated for by a pronounced downward curvature of the ethmoid bloc as seen in *Cyprinion* and *Onychostoma* and, to a lesser extent, in *Varicorhinus* and *Capoeta*. The depressed ethmoid region in *Labeo* and *Garra* possibly fulfills the same function.

The reduced and medially curved mid-lateral ascending maxillary process of *Cyprinion semiplotum* appears otherwise only in *Onychostoma*. In both taxa this feature is apparently correlated with an extensive area of connective and tendinous tissue attaching to the inner face of the 1st infraorbital (see p. 305). The medial notch on the posterior arm of the maxilla in some *Cyprinion* species and in *Capoeta* performs a similar function as a hold-fast for the thick tissue connecting the maxilla with the coronoid process of the dentary (see p. 305).

Concerning the *Cyprinion* lower jaw, the most important evolutionary innovation appears to have been the development of a synarthritic mandibular joint. Such a joint usually suggests some degree of lateral movement, as in the 'knuckle joint' of cynodontine characoids (Howes, 1976), but in the case of *Cyprinion* it may act as a compensatory device to the torque induced by the contraction of the thickly ligamentous *protractor hyoideus* muscle. The absence of any lateral jaw movement is also suggested by the strongly produced lateral and medial anguloarticular processes which provide a rigid coupling with the quadrate.

Changes associated with increased medial curvature of the dentary appear to be manifest in the outward slope of the coronoid process so that the axis and insertion angle of the *adductor mandibulae* A_2 and A_3 muscles remain unchanged. This is contrary to the condition in *Capoeta* where the coronoid process and muscle fibres are set at an angle to the body axis. In *Cyprinion* there is a noticeable change in the relative position of the coronoid process from its mid-lateral point in the plesiomorph *C. acinaces* to a posterior position in *C. semiplotum*. This apparent positional shift is due to morphological changes in the surrounding elements, i.e. broadening and posterior shortening of the anguloarticular and the medial curvature of the dentary (Fig. 16A–E, G–K).

The rigid articulation of the lower jaw in *Cyprinion semiplotum* and *C. burmanica* appears to restrict its vertical movement and it seems merely to act as a firm platform for the highly mobile lip.

The lower lip of *Cyprinion* differs from that in other taxa in being a mobile structure; the epidermis is so loosely attached to the underlying labial shelf that it is free to move antero-posteriorly, and its mobility appears to be controlled by the action of the *protractor hyoideus* complex *via* dorsal and ventral tendinous linkages. This additional function of the *protractor hyoideus* is also indicated by a multi-directional joint between the hyoid and the suspensorium.

Thus, in the more derived *Cyprinion* species, increased complexity of the jaw-quadrate articulatory surfaces and of the lower lip is correlated with increased mobility of the hyoid bar and hypertrophy of the *protractor hyoideus*.

Where it occurs, a sector mouth appears to have the same basic function i.e. for scraping or ploughing epilithic material (see Matthes, 1963). Certainly, there are some 'necessary design components' common to all lineages of taxa with a sector mouth, viz. marked medial curvature of the anterior portion of the dentary; a broadened anguloarticular and barely extending beyond the posterior border of the dentary; greater mobility of the hyoid-suspensorial joint; 3rd branchiostegal ray shifting ventrally to the posterohyal, and an hypertrophy of the *protractor hyoideus* musculature.

Apart from *Cyprinion* such specializations can be found among *Barbus-Varicorhinus* species. Doubtless, cranial and vertebral apomorphies (deepening of the posterior cranial region and increased rigidity of the anterior vertebral column) form a functional unity contributing to epilithic feeding activity. Just how these components interact functionally with those of the jaws, the hyoid and branchial arches, are problems to be solved.

An earlier remark (Howes, 1981) that the '. . . morphology of the lower jaw is possibly the most variable unit in Cyprinidae . . .' is borne out by this study. That the cyprinid jaw appears to be so adaptable suggests that, as in cichlids, the pharyngeal bones perform a dominant functional role of food manipulation and mastication, so freeing the jaws for specialized food gathering. No comparative experimental functional data are available for cyprinid taxa and it is not known whether the pharyngeal apparatus is as versatile as that of cichlids and whether it exerts a primary dominant influence on jaw modification. Liem (1980) has pointed out that in cichlids epilithic feeding patterns are of a kind requiring specializations that exceed those of simple inertial suction feeding. Certainly this appears to be true for sector-mouthed cyprinids as well, where (in the more derived forms) upper jaw protrusion is minimal and the manipulative function of the jaw in food gathering has been transferred, in part, to the hyoid arch.

Synopsis of *Cyprinion* species

The synonymies include only the original citation of the species.

CYPRINION Heckel, 1843

Semiplotus Bleeker, 1863
Scaphiodonichthys Vinciguerra, 1889
Scaphiodontopsis Fowler, 1934

The reasons for synonymising *Semiplotus* with *Cyprinion* have been explained in this paper p. 299).

Scaphiodonichthys was separated from '*Semiplotus*' on the differences in the number of branched dorsal fin rays (9–12 in *Scaphiodonichthys*, 20–25 in '*Semiplotus*'). Smith (1945 : 206) quotes from a letter he received from Dr S. L. Hora who suggested that intermediate forms were '. . . yet to be discovered with a number of branched rays intermediate between 12 and 20. When such forms are found *Semiplotus* and *Scaphiodonichthys* will have to be regarded as congeneric . . .' To my knowledge no such 'intermediate' forms have been found. The existence of synapomorphic osteological and myological characters in species of both '*Scaphiodonichthys*' and *Cyprinion* indicates their generic unity (see p. 312 for a list of characters). When viewed as species of *Cyprinion*, then 'intermediate forms' linking '*Semiplotus*' and '*Scaphiodonichthys*' are in fact present, and indeed the number of branched dorsal fin rays does range from 10–25.

Species occurring east of the Himalayas

Cyprinion semiplotum McClelland, 1839

Cyprinus semiplotus McClelland, 1839 *Asiat. Reschs.* **19** : 374
Cyprinion semiplotus Heckel, 1843 *in* Russegger's Reisen **1** : 1015
Semiplotus semiplotus Bleeker, 1863 *Atlas Ichth.* **3** : 25
Semiplotus mcclellandi Bleeker, 1863 *Atlas Ichth.* **3** : 25
Semiplotus cirrhosus Chaudhuri, 1919 *Rec. Ind. Mus.* **16** : 280

DISTRIBUTION. Nepal, north Bengal (see Hora, 1937; Hora & Gupta, 1940).

Cyprinion modestum Day, 1870

Semiplotus modestus Day, 1870 *Proc. Zool. Soc. Lond.* : 101

Day (1870) considered this species as '. . . intermediate between the genera *Semiplotus* and *Cyprinion*'. Unlike *C. semiplotum* but in common with other *Cyprinion* species, *C. modestum* has a serrated dorsal fin spine. No specimens have been examined in the course of this study (the presumed types are in Calcutta) but according to Hora (1937 : 46) Day's species is 'quite distinct'.

DISTRIBUTION. Akyab Hills, Upper Burma.

Cyprinion burmanica Vinciguerra, 1889

Scaphiodonichthys burmanicus Vinciguerra, 1889 *Ann. Mus. Civ. Storia* Nat. Genova (2) **9** : 285
Scaphiodontopsis acanthopertus Fowler, 1934 *Proc. Acad. Nat. Sci. Philad.* **86** : 119
Onychostoma macroacanthus Pellegrin & Chevey, 1936 *Bull. Soc. Zool. France* **61** (1) : 18–27

Taki (1975) demonstrated an overlap of lateral line scale numbers between *C. burmanicus* and *C. acanthopterum* and stated that the two species were distinguishable only by the number of dorsal fin rays. I find that in a sample of 16 specimens identified as *C. burmanica* (28–65 mm SL uncat. Smithsonian Coll. Upper Thailand), there are nine specimens with 11 and seven with 10 branched dorsal rays. There are thus no meristic differences separating the two 'species'. Since I can find no morphological differences between the syntypes of *C. burmanica* and the series of *C. acanthopterum* studied by Smith (1945), I consider the species to be synonymous.

DISTRIBUTION. Burma, Thailand, Laos, Vietnam.

Species west of the Himalayas

Despite the revision of Berg (1949) and the work of Mirza (1969), many taxonomic problems remain concerning the species in this area. As yet, no author has examined all the nominal types. Also, too few specimens have been examined to judge the degree of intraspecific variability in certain characters.

Cyprinion acinaces Banister & Clarke, 1977

Cyprinion acinaces Banister & Clarke, 1977 *J. Oman Studies* : 123–126

DISTRIBUTION. Saudi Arabia

Cyprinion macrostomum Heckel, 1843; type species of the genus

Cyprinion macrostomum Heckel, 1843 *Ichthyologie* in Russegger's Reisen **1** : 1065
?Cyprinion neglectum Heckel, 1846 *Die Fische Persiens* in Russegger's Reisen **2** (3) : 223
?Cyprinion tenuiradius Heckel, 1846 *Die Fische Persiens* in Russegger's Reisen **2** (3) : 261

Berg (1949) included *C. neglectum* in synonymy without having seen the type and regarded *C. tenuiradius* as a valid species. However, from Heckel's figure *C. tenuiradius* would seem to be simply a 'variant' of *C. macrostomum.*

DISTRIBUTION. Tigris-Euphrates (see Banister, 1980).

Cyprinion kais Heckel, 1843

Cyprinion kais Heckel, 1843 *Ichthyologie* in Russegger's Reisen **1** : 1066
?Cyprinion cypris Heckel, 1843 *Ichthyologie* in Russegger's Reisen **1** : 1067

Berg (1949) included *C. kais* in the synonymy of *C. macrostomum* on the grounds of minor variation in position of the dorsal fin with respect to the pelvic fin insertion (the character Heckel had used to separate the species). Although Berg (1949) recognised differences in mouth shape between the taxa, he obviously considered them to be of little taxonomic worth. I have seen the types of neither *C. macrostomum* nor *C. kais*, and the recognition of these species is based on a comparison of Heckel's (1843) figures with two recognisably distinct taxa represented in the BMNH collections. In *C. kais* the mouth is small, with the keratinized lip of the lower jaw prominent and more upwardly directed than in *C. macrostomum.* Other differences involving the morphology of the jaws and hyoid elements are given elsewhere in this paper.

From Heckel's (1843) figure (Fig. 3, pl. 7) it seems likely that *C. cypris* is synonymous with *C. kais* rather than with *C. macrostomum* as indicated by Berg (1949), and that it represents a juvenile specimen in which the keratinization of the jaw is still incomplete.

DISTRIBUTION. Tigris-Euphrates.

Cyprinion microphthalmum Day, 1880

Scaphiodon microphthalmus Day, 1880 *Proc. Zool. Soc. Lond.* : 227
?Scaphiodon muscatensis Boulenger, 1887 *Proc. Zool. Soc. Lond.* : 665
Cirrhina afghana Gunther, 1889 *Trans. Linn. Soc. Zool.* **5** : 106
Cirrhina afghana nikolskii Berg, 1905 *Ann. Mus. Zool. Acad. Sci.* **10** : 106
Scaphiodon baluchiorum Jenkins, 1910 *Rec. Ind. Mus.* **5** : 124

This synonymy is that of Berg (1949) but appears suspect. The type specimens of *Scaphiodon microphthalmus* are possibly lost (see Banister & Clarke, 1977) and until such time as they reappear certain identification of this species is not possible. However, Mirza's (1969) description based on specimens from Quetta, the type locality, appears to represent the species Day (1880) described. Specimens I have examined from Baluchistan (BMNH

1883.8.2 : 20–26) and the syntypes of *Cirrhina afghana* (BMNH 1886.9.12 : 155–159; 21) conform to Mirza's description and that given by Jenkins (1910) for *Scaphiodon baluchiorum*.

Banister & Clarke (1977) followed Berg (1949) in regarding *Cyprinion muscatensis* as synonymous with *C. microphthalmum*.

Distribution. Baluchistan, Afghanistan, the Indus Plain and Saudi Arabia.

Cyprinion milesi Day, 1880

Barbus milesi Day, 1880 *Proc. Zool. Soc. Lond* : 228
Barbus bampurensis Nikolsky (1899) 1900 *Ann. Mus. St. Petersb.* **4** : 410
Scaphiodon daukesi Zugmayer, 1912 *Ann. Mag. nat. Hist.* **8** : 596
Barbus baschakirdi Holly, 1929 *Anz. Akad. Wiss Wien* **7** : 1
Cyprinion milesi Berg, 1949 *Trudy zool. Inst. Leningr.* **8** (4) : 821

Distribution. West Pakistan and Iran (see Mirza, 1969): BMNH specimens from Afghanistan (1889.2.1 : 263–4) and Dizak, Baluchistan (1883.8.2 : 2–3).

Cyprinion watsoni Day, 1872

Scaphiodon watsoni Day, 1872 *J. Asiatic Soc. Bengal* **41** : 324
Scaphiodon irregularis Day, 1872 *J. Asiatic Soc. Bengal* **41** : 321
?*Cyprinion kirmanse* Nikolski, 1899 *Ann. Mus. St. Petersb.* **4** : 412
Scaphiodon macmahoni Regan, 1906 *J. Asiatic Soc. Bengal* **2** : 8
Scaphiodon watsoni var. *belensis* Zugmayer, 1912 *Ann. Mag. nat. Hist.* (8) **10** : 596
Scaphiodon readingi Hora, 1923 *Rec. Ind. Mus.* **25** : 379–382
Cyprinion watsoni Berg, 1949 *Trudy zool. Inst. Leningr.* **8** (4) : 814

The above synonymy mainly follows that of Mirza (1969) who found a complex overlap of morphometric and meristic characters between *C. watsoni* and *Scaphiodon irregularis*. Certainly, there appear to be no osteological or myological differences between these 'species'.

Scaphiodon macmahoni was included by both Berg (1949) and Mirza (1969) in the synonymy of *Cyprinion microphthalmum*. However, I find that *S. macmahoni* possesses the same mouth morphology and degree of dorsal fin spine serration as does *Cyprinion watsoni* and thus it is included in the synonymy of that species.

Distribution. West Pakistan, Iran and Afghanistan, and the Helmand basin of Baluchistan.

The taxonomic status of *Semiplotus dayi* Fowler, 1958

Fowler (1958) considered that *Scaphiodon aculeatus* of Day (1880) was a misidentification and that the specimens concerned represented a new species of *Semiplotus* for which Fowler (1958) created the species *S. dayi*.

Although Day's specimens can no longer be traced, his description (1880) gives no cause to think that he was not describing *Scaphiodon aculeatus*. Since *Scaphiodon aculeatus* (Val. 1844) is a synonym of *Capoeta capoeta* (see Karaman, 1969) it follows that *Semiplotus dayi* must also become a synonym of that taxon.

Relationship of the genus *Cyprinion*

In this study the presence of a sector mouth in various cyprinid taxa is seen both as a character indicating relationship (synapomorphy) and as one independently evolved as a parallelism. Taki (1975) used mouth morphology, degree of dorsal fin spine serration and ossification, and the presence or absence of barbels as the criteria for determining relationships amongst 'semiplotine' genera. Taki considered *Onychostoma* closely related to '*Semiplotus*', '*Scaphiodonichthys*', *Scaphiodon* and *Scaphiognathops*. On the basis of these supposed relationships he recognised an *Onychostoma* group and constructed an elaborate dispersal hypothesis to explain the distribution of the included genera.

Taki (1975) supposed that the onychostomine genera were '. . . derived from *Barbus-Varicorhinus* stock'. As he indicated the group's 'origin' to have been in northern Asia, I take it that he was referring to Euroasiatic *Barbus* and that his '*Varicorhinus*' was in fact *Capoeta* (see Karaman, 1969). Taki further confuses the issue by referring both the middle Asian and western Indian species to *Scaphiodon* thereby implying their monophyly. In fact, Taki's middle Asian '*Scaphiodon*' are all *Cyprinion* species and those along the western Ghats of India are *Osteocheilus* (see Hora, 1942, for synonymies).

The remaining genus included in Taki's *Onychostoma* group is *Scaphiognathops*. Osteological data on this taxon are completely lacking; examination of the type specimen of *S. stejnegeri* (USNM 90303) reveals a quite different jaw morphology to that of any *Cyprinion* species (see figures in Smith, 1931 and Taki, 1974), or for that matter, from any *Onychostoma* species.

Taki's (1975) hypothesis of relationships and dispersal are falsified by the conclusions of this study, namely: **1**. That *Semiplotus, Scaphiodonichthys* and *Scaphiodon* (part) are all synonymous with *Cyprinion*; **2**. That there are no synapomorphies linking *Cyprinion* with *Onychostoma* or with *Capoeta*.

The relationships of *Cyprinion* are still in doubt and the sister-group remains unidentified. This is due to lack of comparative anatomical data for the corpus of species currently referred to the genus *Barbus*. Initial researches cast doubt on the assumed monophyly of *Barbus* and also indicate one group within the complex which could be the sister lineage to *Cyprinion*. The taxa involved are the north African species *B. luteus, B. paytoni, B. callensis, B. waldoi, B. rothschildi* and *B. sharpyei*. In particular '*Barbus*' *paytoni* possesses cranial and jaw features similar to those of *Cyprinion* viz. deep and ventrally curved ethmoid bloc, transverse dilatator fossa, an almost identical posterior neurocranial morphology, broad and deflected labial surface on the dentary, and a broad anguloarticular facet. The shape of the quadrate, the hypertrophy of the interhyal, and the inward curvature of the interoperculum appear to be further indications of relationship. More research is however, necessary to test the hypothesis that the north African '*Barbus*' species group is itself monophyletic.

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